THE SOCIAL FORAGING NICHE OF THE MBENDJELE BAYAKA

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I, James Thompson, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the work

Abstract

This thesis addresses the question of how a population of modern hunter-gatherers, the Mbendjele BaYaka, utilise social behaviours to exploit high quality but difficult to acquire foods. In contrast to other primates, the human diet contains a high proportion of meat, tubers and honey which have in common not only a very high calorific density but also considerable acquisition costs. The theory that human cognition coevolved with a transition to a diet specialising in these resources is far from novel. However, the underlying proximate mechanisms that allow hunter-gatherers to exploit these foods is poorly understood. It is widely accepted that food sharing by hunter-gatherers acts as a form of reciprocal altruism, reducing the risk inherent to high variability foods such as large game. However, the underlying mechanism which maintain the reciprocity are often ignored, simply assuming humans have the capacity to calculate and act upon inequalities. Similarly, a long-standing theory explaining the extended period of juvenile dependence in humans argues that it provides the opportunity to acquire the skills and knowledge necessary to hunt and gather difficult to acquire foods, yet we still no relatively little about how hunter-gatherer children learn and develop.

In this this thesis I address not only the well-worn question of the ultimate explanations for sharing and childhood, but also examine the proximate mechanisms underlying cooperation and social learning. I make use of a range of data on three contemporary Mbendjele camps, which offer varying social structures and levels of market integration, and compare this to previously published data on the Mbendjele as well as data on a contemporary population of fisher-gatherers, the Agta of the Philippines.

The Mbendjele in this study live within a logging concession, an area that in recent years has undergone rapid development. This provides an opportunity to study the impact changes in economy have had on foraging and food sharing. In combination with analyses

that make use of recent innovations in remote sensing technology and social network analysis to examine how kin and social relations facilitate cooperation, I find evidence that food sharing serves multiple functions in this society, one of which is risk reduction, but also that attitudinal reciprocity rather than calculated reciprocity may be the underlying mechanism.

By observing how Mbendjele children spend their time and how this differs with both age and sex I find evidence that learning is a primary motivator of children's activity. However, I challenge the assumption that direct experiential learning of male specific foraging is the main mode of learning for Mbendjele boys, suggesting that either learning is indirect and reliant on horizontal pathways, or that this type of learning is not the primary cause for the evolution of the extended juvenile period in humans.

The key findings of this thesis highlight the important role played, not only by social behaviours, but also social structures in the hunter-gatherer economy. Affiliative relationships stabilise cooperation and facilitate social learning, and a greater understanding of the proximate mechanisms surely offers a pathway to a better understanding of human evolution.

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1. The social foraging niche

The theory that a human diet specialising in high quality foods co-evolved with our increased cognitive ability is far from novel, and below I discuss how this idea has developed over the last 150 years. A current consensus, rarely stated but often implicit in much of the research in this area, is that foods such as meat, tubers and honey offer several advantages over lower quality plant foods more typical of a primate diet, but can only be successfully exploited thanks to the human capacity for social learning and cooperation, in short, our sociality. The central question of this thesis is how exactly is sociality used by a group of modern hunter-gatherers to exploit high quality foods? This question has been relatively poorly explored, perhaps because of its apparent triviality. It is clear that hunter-gatherers, or in fact any human society, are reliant upon social learning and cooperation to acquire the skills, knowledge and materials necessary to subsist. Nevertheless, the precise mechanisms underlying both cooperation and learning are underexplored, particularly in evolutionary anthropology with its focus on ultimate explanations.

Since at least the time of Darwin (1871), the importance of diet to human evolution has proven a perennial topic of debate. Humans and our extinct ancestors have been variously described as killers (Dart 1953), scavengers (Binford 1985) and cooks (Wrangham et al. 1999), traits argued to be relevant not only to the evolution of human diet and subsistence, but to the full suite of cognitive, social and cultural traits which distinguish humans from other primates. It was the discovery of animal remains in association with australopithecine fossils, exhibiting signs of butchery, which prompted Dart's (1953) killer-ape theory of human evolution. According to Dart, not only did the Australopithecines differ from extant non-human primates

in their diet, favouring meat over the more usual fruits and leaves, but the transition to a predatory niche also explained the evolution of bipedalism and tool use. Furthermore, Dart argued that adaptation to hunting was linked to the "loathsome cruelty of mankind" (Dart 1953), which he saw as a trait self-evidently unique to humans. Whilst much of what Dart proposed has fallen by the wayside, the idea that carnivory played an integral role in human evolution has proven more resilient, whether the meat be acquired through hunting (Hill 1982) or scavenging (Binford 1985). Dart's focus on human nature was replaced by theories proposing that hunting was a central driver of human social evolution, leading to male provisioning and stable pair bonds (Hill 1982). The notion that carnivory alone differentiates the human diet from that of other primates has been challenged on two fronts. Predation amongst non-human primates is not as rare as it was once believed. Perhaps most famously, chimpanzees are known to hunt other primates cooperatively (Boesch & Boesch 1989) and less complex forms of hunting have been observed in species such as olive baboons (*Papio anubis*) (Sommer et al. 2016). Additionally, a shift in emphasis in hunter-gatherer studies away from hunting and men's roles towards a broader perspective led to a much-needed focus on the importance of women's work in these societies (Lee 1968). This led to interest in the total breadth of hunter-gatherers diets and theories proposing that food such as yams (Laden & Wrangham 2005) and honey (Crittenden 2011) may have played as important a role in human evolution as meat. As a result, a more nuanced view of the differences in the diet of humans and other primates has emerged, stressing the importance of high quality but hard to acquire foods in the human diet (Kaplan et al. 2000). In comparison to the fruit and foliage which make up the majority of the diet of other apes; meat, honey and importantly tubers are relatively

difficult to acquire but of high quality. They are calorie dense and in the case of meat, fish and invertebrates provide a range of other important nutrients.

For many, this hard to acquire high quality niche not only defines human foragers but explains much about human evolution. Some have argued that, by exchanging plant foods for animal foods, humans were able to reduce dramatically the metabolic investment in digestion and simultaneously invest greater amounts in brain tissue (Aiello & Wheeler 1995). Whilst this hypothesis has been subsequently challenged by empirical data (Navarette et al. 2011), competing "expensive tissue" hypotheses propose that increased energetic costs of the brain are met by behavioural and ecological adaptations rather than physiological trade-offs (Isler & Van Schaik 2014). Beyond the expensive tissue hypothesis, the hard to acquire high quality niche has been much discussed in relation to life history (Hawkes et al. 1998, Kaplan et al. 2000). Amongst almost all non-human mammals, individuals become responsible for feeding themselves upon weaning. In contrast, human children, including in foraging societies, produce less energy than they consume until they reach reproductive age (Kaplan et al. 2000). Then on reaching adulthood, human foragers are able to produce large energy surpluses. This distinctive production curve clearly requires the flow of resources from net producers (adults) to net consumers (children). The question of who provisions children in forager societies remains a topic of debate, in particular, the relative importance of fathers and grandmothers. In light of the apparent inefficiency of big game hunting, in combination with a depiction of food sharing as non-contingent on any future returns, the importance of paternal provisioning has been challenged (Hawkes et al. 1991). In the face of evidence that male foraging is efficient (Gurven & Hill 2009), even amongst the Hadza (Marlowe 2003), and given our more sophisticated understanding of food sharing (see chapter 5 for a review), a provisioning

function of male foraging is strongly supported. The importance of non-parental kin for child survival shows considerable cultural variation (Sear & Mace 2008) and likely varies with subsistence type. In foraging societies, transfer of food between extended kin is common and exhibits signals of provisioning, for instance unbalanced sharing between generations of a family (Hooper et al. 2015, Dyble et al. 2016), though to some extent this is confounded by reciprocal sharing between relatives (Allen-Arave et al. 2008, Nolin 2010). Male provisioning is often discussed in relation to the evolution of pair bonding and monogamy (Lovejoy 1981 , Marlowe 2003), while grand maternal provisioning is argued to have played a role in the evolution of human's slow life history, in particular the long female post reproductive period (Hawkes et al. 1998). Undoubtedly, both parental and extended kin provisioning occur in foraging societies. What is unclear is whether they have played these particular evolutionary roles.

In addition to predictable shortfalls related to life history, it has been suggested that a focus on high quality foods also creates unpredictable shortfalls (Kaplan & Hill 1985). Foods such as meat and honey tend to be encountered sporadically, but once located they can be the source of a large number of calories. Thus, targeting these types of food can produce large variances between the amount of food held by individuals and it is this, some suggest, that leads to food sharing in forager societies (Blurton Jones 1984, Kaplan & Hill 1985, Gurven et al. 2000).

To summarise, what distinguishes the diet of human foragers from other primates is their focus on high quality but difficult to acquire foods. Two important consequences of this niche are: 1. predictable life history related shortfalls in production and 2. high short-term variance in resource holdings. Links between a change in diet and cognitive evolution have been well

supported for quite some time (Aiello & Wheeler 1995). Subsequent work has further developed this theory by highlighting the social solutions to the challenges imposed by the human diet. This paints a picture of humans as inhabiting a unique "social foraging niche". The difficulties in acquiring game, honey and underground storage organs are not simply overcome by our large brains. Rather, foragers also rely on those around them as sources of aid and knowledge. In the following section I highlight the social foraging strategies adopted by human foragers and contrast this to selected non-human animals. I begin by discussing cooperative foraging before moving on to discuss the influence of social learning.

1.1 Cooperative foraging

Human foragers exhibit at least three distinct forms of cooperative foraging; direct cooperative foraging, a division of labour and provisioning/sharing.

Direct cooperative foraging

By direct cooperative foraging I mean the direct participation of multiple individuals in the acquisition of resources. Whilst a true division of labour and sharing are relatively rare or absent amongst non-human animals, direct cooperative foraging is common. Chimpanzees hunt other primates in groups, with certain individuals acting to flush out the prey whilst others lie in ambush (Boesch & Boesch 1989). Similarly, a number of cetacean species exhibit a range of quite sophisticated group hunting techniques (Gazda et al. 2005, Pitman & Durban 2011) and for social carnivores such as lions (*Panthera leo*) and hunting dogs (*Lycaon pictus*) social hunting is effectively obligate (Stander 1992, Creel & Creel 1995).

For humans, hunting is also the most common form of cooperative foraging. For example, net hunting by central African Pygmies involves the cooperation of a large number of people of both sexes and across age groups (Bahuchet 1985, Noss 1997). Cooperative foraging for non-meat foods is rare in non-human animals. Whilst social foraging is common in groups such as primates and ungulates, in these cases each individual is solely responsible for their own production but group together for other reasons, for instance - to reduce predation (Hill & Lee 1991), avoid infanticide (Harcourt & Greenberg 2001) and protect against parasites (Mooring & Hart 1992). When female hunter-gatherers forage they typically do so in groups. Whether this is social or cooperative foraging is unclear. Honey collection is an overt example of non-hunting cooperative foraging. For example, amongst the Mbendjele, one man may climb the tree to reach the beehive whilst another remains on the forest floor, preparing the bundles of smoking leaves they use to subdue the bees.

Division of labour

In the above examples of cooperative hunting we can identify cases of role specialisation. In net hunting, certain individuals act as beaters, chasing the animals towards the nets whilst others wait to quickly grab and kill animals that become snagged (Bahuchet 1985, Noss 1997). This is strikingly similar to the roles adopted by chimpanzees when hunting monkeys. Whilst short-term specialisations can be found in non-human animals, we do not observe the long-term divisions of labour that are prevalent in all human societies. The most striking example of a division of labour, particularly in foraging societies, is the sexual division of labour. The notion that men are hunters and women gatherers is clearly a simplification belying the large cultural variance in foraging behaviour. For example, women in a number of foraging societies are

known to hunt (Noss & Hewlett 2001, Marlowe 2007, Bliege Bird & Bird 2008) and men frequently engage in gathering. Nevertheless, sexual variation in foraging is widespread in hunter-gatherer societies (Marlowe 2007, Codding et al. 2011).

It is possible that sexual variation in foraging is not actually a form of cooperation, rather it is the result of women and men pursuing different goals. Evidence from the Hadza (Hawkes et al. 1991) and Meriam (Bliege Bird et al. 2001) has been used to suggest that men's foraging effort is motivated by signalling rather than provisioning. This theory has been challenged based on data from other societies (Gurven & Hill 2009) and a reappraisal of the Hadza example (Wood & Marlowe 2013) and currently there is a compelling body of evidence that men's foraging effort is a form of provisioning, though this doesn't entirely preclude the possibility that it also serves a as a signal. If both men and women are motivated to forage as a way of gaining resources, we must consider what the benefits of such a strict division of labour are, whether this is a product of the particular human diet and consider its impact on human evolution.

There are two, non-mutually exclusive, explanations of the sexual division of labour in foraging societies. Firstly, constraints on women preclude them from participating in hunting (Hurtado et al. 1992). Secondly, if foraging strategies require a large initial investment before an efficient level of productivity is reached, swapping between strategies becomes costly, favouring specialisation. Both these hypotheses suppose there is value in a broader diet, or in the case of the constraint model, that meat has value above that of other foods. Some comparisons of male and female productivity suggest that hunting may be a more efficient source of calories (Kaplan et al. 2000) and meat offers an excellent source of protein as well as a range of micronutrients such as zinc and iron (Pereira & Vicente 2013). Furthermore, a broad diet has

benefits beyond the extended nutritional range, as the variance in productivity between different resources is likely to have a degree of independence. By focussing on different strategies, a husband and wife can reduce the risk of a food shortfall on any given day.

It is possible that the sexual division of labour is specifically adapted to the human dietary niche. If hunting requires considerable investment, in terms of learning and/or physical development (Kaplan et al. 2000) then this could explain why we see specialised foraging roles. On the other hand, the division of labour could be entirely a product of constraint on women, a consequence of the demands of child rearing (Hurtado et al. 1992). In this case the division of labour may have evolved as a response to changes in human life history.

Provisioning/sharing

In most animals, provisioning occurs only between parent and offspring and only during very early life. For instance, chimpanzees become solely responsible for their own food upon weaning (Kaplan et al. 2000). In contrast, humans continue to provision their children throughout childhood. Furthermore, in forager societies a large component of an individual's diet, be they child or adult, is likely to come from outside their household, provided by both kin and non-kin. Food sharing has been found in a large number of forager societies including; South American horticulturalists (Kaplan et al. 1985, Gurven et al. 2001, Hames & McCabe 2007, Koster 2011), Central African Pygmies (Bahuchet 1990, Kitanishi 1998), Inuit (Kishigami 2000), Siberian foragers (Ziker & Schnegg 2005), the Hadza (Hawkes et al. 2001) and a number of marine foraging groups (Bird et al. 2002, Nolin 2010, Dyble et al. 2016). The apparent ubiquity is a clear indication that food sharing is a product of the foraging way of life. This has led to a tendency to generalise sharing across all societies (Gurven 2004a, Jaeggi & Gurven

2013). In reality, food sharing is multifaceted and there is no single explanation for all food transfers (Hooper et al. 2015, Dyble et al. 2016, Jaeggi et al. 2016). Kin provisioning (Hawkes et al. 2002) may very well serve a separate purpose to sharing between unrelated households (Gurven 2004). That being said, it is likely that all such transfers are a result of the focus on difficult to acquire foods, hence its prevalence in a diverse range of foraging societies. I have previously mentioned that high quality but difficult to acquire foods produce a distinctive production curve over the life course (Kaplan et al. 2000). It has been suggested that in combination with the constraints of pregnancy and child rearing on mothers, this produces periods of predictable food shortfalls that have to be buffered by provisioning by kin, be it the father (Marlowe 2003) or grandparents (Hawkes et al. 2002). Additionally, a focus on sporadically acquired but large package size resources such as game has the potential for unpredictable shortfalls in resources which may lead to the transfer of food between unrelated households in a camp as a product of either tolerated theft (Blurton Jones 1984, Winterhalder 1996) or reciprocal altruism (Gurven 2004a).

1.2 Social learning and culturally facilitated foraging

Clearly cooperation is critical to the exploitation of hard to acquire foods by hunter-gatherers. However, I have already touched upon the importance of social learning. I have suggested that what distinguishes direct cooperative foraging by humans from that of animals such as lions is a greater reliance on social learning. Similarly, I have suggested that one potential cause of the sexual division of labour is that learning how to forage requires a large investment. It is not necessary that this learning be socially acquired, but given the clear cultural signature of hunting practices this is a reasonable assumption.

Social learning is not uniquely human. The famous waggle dance used by honey bees (*Apis mellifera*) to direct hive mates to nearby food sources presents a vivid example of socially transmitted information aiding foraging (von Frisch 1946). Many of the cultural markers in chimpanzees are related to foraging, be they nut cracking (Boesch & Boesch 1982), or dipping for ants (McGrew 1974). Recent evidence has even suggested that teaching may play a role in the transmission of some of these foraging techniques (Musgrave et al. 2016). It is interesting to note that both examples of socially facilitated foraging in chimpanzees, cooperative hunting and tool use, provide chimpanzees with access to foods of higher nutritional quality than their typical diet of ripe fruit. Whilst the high-quality features of foods are relatively easy to describe in terms of nutritional content, precisely what is meant by "hard to acquire" is more difficult to discern. Previous attempts have defined this property as a single quantity, e.g. "skill requirement" (Kaplan et al. 2000). In actuality, foraging costs are the product of a number of factors. For example, the costs to extract ripe fruit, a favoured food of chimpanzees (Newton-Fisher 1999), are probably no higher than for the extraction of unripe fruits but the former may incur greater search costs if the distribution is patchier or of a lower density. If we consider those foods targeted by human foragers; game, fish, and tubers, such foods probably incur relatively high search and extraction costs (Figure 1.). It is clear that culture and social learning are integral to humans reducing extraction costs. Pygmies are only able to hunt game as large as elephants (*Loxodonta africana*) because of the spears they fashion (Janmart 1954), whilst the Hadza have traditionally relied upon bows and poison tipped arrows to hunt the large ungulates of East Africa (O'Connell et al. 1988). A less obvious effect is the reduction of search costs through information exchange. Such processes are thought to occur in severall non-

human central place foraging species (Wilkinson 1992, Marzluff et al. 1996, Weimerskirch 2010) but have not been explored in human populations.

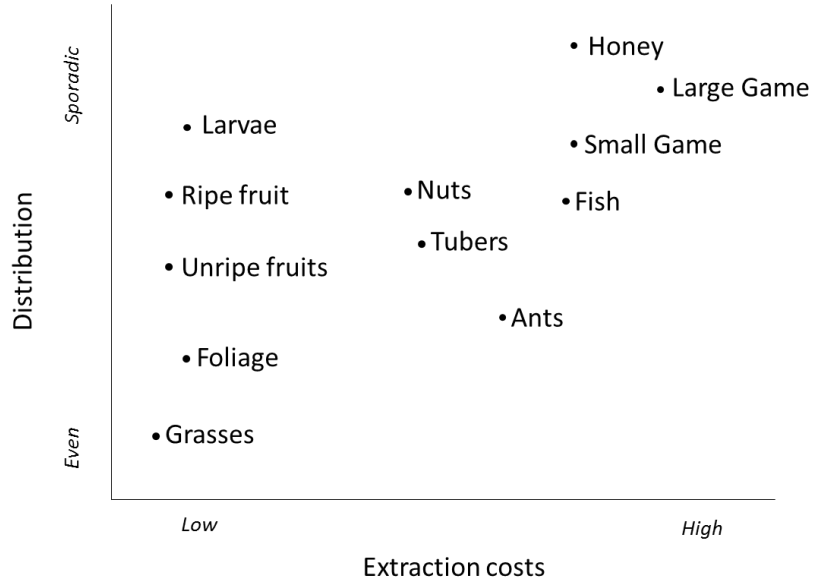

Figure 1.1. Theoretical representation of estimated foraging costs of foods as a product of spatiotemporal distribution and extraction cost. Extraction costs can be thought of in terms of energetic or opportunity costs.

Social learning and cumulative culture are clearly powerful tools and, as many have suggested (for example Boyd et al. 2011), surely account for the wide range of environments in which we find human foragers. Whilst examples of social learning can be observed in a range of species, for example chimpanzees (Musgrave et al. 2016), Caledonian crows (Holzhaider et al. 2010) and even insects (Leadbetter & Chittka 2007), the lack of cumulative culture in non-human animals clearly speaks to significant costs and constraints. The cognitive, social and behavioural requirements for cumulative culture are much discussed (Tomasello 2009, Dean et al. 2012,

Lewis & Laland 2012) and a full review falls outside the scope of this thesis. However, the application of social learning specifically to subsistence entails a cost which is of relevance. If learning is a requirement of foraging, then efficiency is inherently tied to experience. It is this, which Kaplan and colleagues (2000) suggest, explains why children in foraging societies are unable to produce enough food to support themselves. Competing explanations for the low levels of production amongst hunter-gatherer children are discussed fully in chapter 7, but include physical constraints (Blurton Jones & Marlowe 2002) and low foraging effort, resulting from high costs or small benefits of child foraging (Blurton Jones et al. 1994, Tucker & Young 2005).

I have argued that what differentiates human subsistence from that of other animals is both the high quality resources targeted and the reliance on cooperation and social learning to acquire them. In trying to separate cooperative and cultural adaptations to the human dietary niche it has become clear that this is a false dichotomy. Cooperative foraging is socially learnt and a reliance on cumulative culture imposes demands that are met cooperatively, be that through a division of labour or food sharing. The likelihood that the human capacity for cooperation and cumulative culture coevolved is further strengthened by their relation to cognition. The abilities to recognize individuals, overcome temporal discounting, remember past interactions and exchange information are just some of the abilities that have been suggested to allow humans to engage in non-mutual cooperation but which are beyond other animals (Stevens et al. 2005, Clutton-Brock 2009, Melis & Semmann 2010). It is easy to see how some of these, notably memory and information exchange, could also facilitate cumulative culture. That such a broad range of cognitive capacities are discussed in regards to cooperation

and social learning reflects our relatively limited understanding of the proximate mechanisms underlying these phenomena.

1.3 Proximate explanations of cooperation

Much work on cooperation has focussed on ultimate explanations, building on the theories of Hamilton (1964) and Trivers (1971) in identifying the fitness costs and benefits of cooperation. Recently there has been a growing interest in the proximate mechanisms underlying cooperation, particularly that between unrelated individuals, in both humans and other animals. Much of the work regarding humans has focussed on the roles punishment and assortativity play in stabilising cooperation at a population level. Both punishment and assortativity overcome the free-rider problem by ensuring that the net benefits to defectors and cheats are low. This is done by either conferring high costs via punishment (Boyd & Richerson 1992, Boyd et al. 2012), or lowering benefits received by cheats by preferentially directing altruistic acts towards co-operators (Apicella et al. 2012, Lewis et al. 2014).

In contrast, work on non-human animals has attempted to find the conditions under which reciprocity can emerge at a dyadic level (Brosnan & De Waal 2002, Schino & Aurelli 2010, Jaeggi et al 2013). This work has given rise to three theoretical mechanisms underlying reciprocity which, in order of increasing cognitive demands, are; symmetry based reciprocity, attitudinal reciprocity and calculated reciprocity (Brosnan & De Waal 2002, Schino & Aurelli 2010). Symmetry based reciprocity could emerge when animals direct acts of altruism towards group mates based on symmetrical relationship characteristics. For instance, if individuals more frequently interact with others of a similar rank in the dominance hierarchy, then a high degree of reciprocity in behaviours such as allogrooming might arise in the absence of actual

contingency. Attitudinal reciprocity (sometimes referred to as emotional reciprocity) refers to a system where altruistic acts engender positive emotions which in turn encourage reciprocation of the act. Calculated reciprocity requires the actors to keep track of cooperative interactions and to alter their behaviour based on an overt understanding of the costs and benefits. It has been argued that attitudinal reciprocity is well within the capabilities of many primate species (Schino & Aurelli 2010), requiring as it does, simply the ability to form and update social relationships based on interactions. The prevalence of hierarchies, alliances and other social relationships within primates are strong support for this theory. Examples of reciprocity in wild primates in regards to allogrooming (Schino and Pellegrini 2009) and support in antagonistic interactions (Cheney et al. 2010) are likely the result of attitudinal reciprocity.

Evidence for calculated reciprocity in non-human primates is limited to a small number of species, namely chimpanzees (Brosnan et al. 2009) and orangutans (*Pongo pygmaeus*) (Pele et al. 2009) and even within these species only a very small number of dyads exhibited this behaviour under experimental conditions. The limited ability for non-human apes to engage in calculated reciprocity could explain the differences in cooperation by humans and other species. However, there is relatively scant evidence that naturally occurring reciprocity in humans is the result of calculated reciprocity. In part this is a product of the focus on the aforementioned group scale mechanisms such as punishment. However, it is clear that much of the cooperation in humans is not of the generalised form we would expect from such mechanisms. Food sharing is a clear example of this. Food is not shared indiscriminately between all camp members, but is targeted at specific other individuals (Kitanishi 1998, Nolin 2012, Koster & Leckie 2014, Koster et al. 2015, Dyble et al. 2016). Thus, the proximate

mechanisms underlying this form of cooperation are likely to be calculated or attitudinal reciprocity. The lack of discussion of these mechanisms in relation to food sharing is the result of an assumption that calculated reciprocity is the underlying mechanism. However, the fact that humans are capable of the mental bookkeeping necessary to keep track of the costs and benefits of cooperation does not mean simpler mechanisms may not also be at work.

1.4 Proximate mechanisms of social learning

Compared to cooperation, the proximate mechanisms of social learning have long been a topic of interest. Early work on the subject identified mechanisms of learning as a way of differentiating social learning from asocial learning (Galef 1976). Soon interest switched to identifying and classifying different forms of social learning with a focus on differences between social enhancement and observational learning (Heyes 1994). The former category includes cases where the activity of one individual alters the environment or encourages access to stimuli which then facilitate individual learning.

A classic, though controversial, example of this has been the practice of milk bottle opening, observed amongst wild blue tits (*Cyanistes caeruleus)*, and experimentally stimulated in captive chickadees (*Parus atricapillus*). It has been argued that the rapid spread of bottle opening in a number of wild bird populations was the result of social learning (Fisher & Hinde 1949), specifically that on exposure to an opened milk bottle a naïve individual is able to learn how to open it for themselves without having to first observe another bird (Sherry & Galef 1984). This contrasts to examples of observational learning, where seeing a model engaged in the activity is a requirement of its transmission.

Attempts to test whether tool use in chimpanzees were transmitted by observational learning or social enhancement proved that observational learning is not a single mechanism (Tomasello et al. 1987). Chimpanzees exposed to a tool using individual fared better in a simple task than did the group only exposed to the tools. However, those chimpanzees who adopted tool use did not actively copy the experienced models movements, just their use of the tool in general.

Such evidence has given rise to distinction between observational learning as emulation, such as that shown by the chimpanzees, and imitation, cases where the specific actions of the model are adopted by the naïve subject. The distinction between emulation and imitation has received considerable attention in light of experiments which find that the latter is rarely if ever used by chimpanzees but commonly used by human children (Nagell et al. 1993). Initial interpretation of these results positioned emulation as just a small step beyond social facilitation (Tomasello et al. 1987), with the implication being that it is less cognitively demanding than imitation. However, experiments which showed that under certain conditions chimpanzees will exhibit imitation (Horner & Whiten 2005, Whiten et al. 2009) have challenged this theory, instead suggesting that humans may over-imitate at the cost of efficiency.

Running parallel to the classification of social learning has been a debate regarding from whom individuals tend to learn. Examination of the relationship between model and learner has led to the development of a tripartite system of classification. Learning can be horizontal - between peers, vertical - between parents and offspring, or oblique - between generations but not parent and offspring (Cavalli-Sforza & Feldman 1981). The validity of separating vertical transmission from other forms of inter-generational transfer (oblique transmission) came from

evidence that a considerable amount of certain types of knowledge can be ascribed to this pathway, both in industrial (Cavalli-Sforza et al. 1982) and hunter-gatherer societies (Hewlett & Cavalli-Sforza 1986). Since the work of Cavalli-Sforza and colleagues, a considerable body of literature has emerged identifying the most important mode of transmission and how this varies for different forms of knowledge. The predominance of one mode of transmission over another may be the product of circumstance. For example social learning in Aka children under the age of 5 was found to be largely vertical, whereas for children between 6 and 12, horizontal and oblique transmission were found to play a larger part (Hewlett et al. 2011). This may simply reflect changes in a child's social network, becoming exposed to an increasing number of individuals beyond their immediate family with age. Similarly, the fact that Mbendjele more commonly share knowledge regarding medicinal plant use with family than other camp members may reflect the fact that most medicine is practised within the household and thus individuals are more likely to be exposed to the medicinal knowledge of kin (Salali et al. 2016). Alternatively, the greater importance of one mode of transmission may reflect some form of optimisation, particularly in regards to a bias towards kin. Kin may serve as a better model if the behavioural variants are sensitive to genotype (Laland 2004). To illustrate this we can return to the example of medicinal plant use by the Mbendjele. If the efficacy of medicines correlated strongly with genotype then one is better off adopting those plants used by people with a high likelihood of sharing the critical genes, i.e. kin. Of course, a bias towards kin need not be optimal in each specific circumstance, a few such cases could lead to a generalised preference for kin to evolve. However, the fact that kin biases are observed for some forms of knowledge but not others, for instance ritual plant use by the Mbendjele (Salali et al. 2016), suggests this is not the case.

As previously discussed, many have suggested that learning is of critical importance to the human foraging niche (Kaplan et al. 2000) and in some cases, for instance the Tsimane, it has been shown that experience positively correlates with foraging efficiency (Gurven et al. 2006, Schniter et al. 2015). Yet little is known about how hunter-gatherer children acquire foraging skills and from whom they do so. The previously discussed study on plant use by the Mbendjele found that plants involved in foraging, for instance poisons used for hunting and fishing, were no more commonly shared by kin than unrelated camp members (Salali et al. 2016), suggesting that at least in this specific case, horizontal and/or oblique transmission of knowledge is important. In contrast a detailed analysis of acquisition of knowledge pertaining to honey collecting amongst the Jenu Kuruba found that vertical transmission was of greatest importance (Demps et al. 2012).

1.5 Conclusion and summary of thesis structure

The foraging niche of humans differs from other primates in the focus on high quality but difficult to acquire resources. These two traits combine to create distinctive patterns of variance in production, these are unpredictable short-term variance and predictable long-term periods of deficit and surplus over the life course. Whether the transition to this niche selected for humankind's distinctive capacities for cooperation and social learning, or whether this evolved prior to a shift in diet, it is clear that human foragers are reliant on cooperation and culture to exploit this niche successfully.

Cooperation and culture provide greater access to difficult to acquire foods through cooperative foraging and the tools and strategies that are the product of cumulative culture. Furthermore, they provide methods to buffer the high variance in production. Food sharing is

ubiquitous amongst foragers; and the relative importance of kin provisioning, as a solution to long term variance, versus reciprocal sharing as a buffer to short term risk, is an area of ongoing debate. Additionally, the proximate mechanisms underlying food sharing are not well understood. I suggest that, given the non-generalised form of sharing most commonly reported, a dyad specific approach, similar to that which has been applied to cooperation by nonhuman primates, may be more profitable than the more typical discussion of punishment and assortativity found in the anthropological literature. Evidence of calculated reciprocity under natural conditions could lend weight to the argument that cognitive constraints prevent the types and amount of cooperation we see in humans from occurring in other species.

The high quality but hard to acquire depiction of human diet has proven an invaluable jumping off point for a range of theories but provides an overly simple characterisation. In particular, the precise costs of foraging and exactly why certain foods are hard to acquire are poorly understood. Since it has been suggested that it is this which leads to the distinctive production curves over the life course, a better understanding of the costs and constraints has the potential to inform our understanding of the evolution of human life history. In this thesis I address the consequences of variance in the human diet for cooperation, assess the ultimate and proximate explanations of food sharing and evaluate the constraints of foraging, by examining the subsistence practices of a contemporary population of hunter-gatherers, the Mbendjele BaYaka of Republic of Congo.

Chapter 4 provides detailed quantitative data on the subsistence of contemporary populations of Mbendjele BaYaka and assesses the impact of market integration on their diet, foraging and food sharing. As well as providing the ethnographic context for the rest of the thesis, this

chapter addresses the question of whether extant populations of hunter-gatherers still conform to the social foraging niche, thus informing their use as a model for ancestral populations. I compare previously published data on the Mbendjele with data collected from current populations with varying levels of market exposure. In particular, I examine whether trade and agriculture have reduced levels of cooperation in Mbendjele camps as a product of reduced variance in production.

Chapter 5 extends the analysis of cooperation further and attempts to explain the function Mbendjele of food sharing and whether this has changed as a result of market integration. In particular, I examine whether meal sharing by the Mbendjele is a product of kin selection or reciprocal altruism.

In this introduction I have stressed the roles of cooperation and social learning in the exploitation of the complex foraging niche. But sociality goes much beyond this. Group living comes with costs and new evolutionary pressures. Whether selection for cooperation and learning selected for human social structure, or whether structure was a precondition for these behaviours to evolve is a difficult question to answer. However, social network analysis provides us with tools which allow us to examine the interactions between social structures and social behaviours. In chapter 6 I extend the analysis of meal sharing from the previous chapter by comparing networks of meal sharing with other Mbendjele social networks. I firstly address methodological questions on how different types of social network can be used in the study of naturally occurring populations. I then address the questions of whether position within a social network affects an individual's involvement in food sharing and whether social interactions facilitate the transfer of food. In doing this I aim to elucidate the importance of

partner choice in food sharing and further elucidate the proximate mechanisms underlying this behaviour.

The importance of social learning and cumulative culture to foraging is self-evident; an Inuit supplanted to the Congo would struggle to feed himself as much as an Mbendjele in the Arctic Circle would. What remains to be discovered, though, is the impact that this has had on human evolution. I have suggested that the sexual division of labour is the result of a need to specialise. Furthermore, I have highlighted the theory that the distinctively human low levels of foraging productivity during childhood result from a need to learn first how to hunt and forage. Both hypotheses suggest that learning should play a critical role in foraging efficiency and that hunter-gatherer children should invest heavily in learning the sex specific skills they will draw upon as an adult. In chapter 7 I test these hypotheses by examining the activity patterns of Mbendjele children. I examine whether Mbendjele children make a meaningful economic contribution and whether skill or physical constraints play a larger part in determining their contribution.

2. Study Population

The Mbendjele Bayaka, also referred to as Mbenzele (Bahuchet 2012) or simply Aka (Kitanishi 1997), are a dialect group of the larger Aka linguistic group of Pygmies. They reside in Northern Republic of Congo in the Sangha and Likoula departments. The Aka's total range extends into southern Central African Republic (CAR) (figure 1).

Figure 2.1. Map of Republic of Congo showing the distribution of the Aka (highlighted in blue). Adapted from Bahuchet 2012 (Google Earth 2016).

2.1 Central African Pygmies

The term Pygmy has been used for well over a century to refer to the groups of rainforest dwelling hunter-gatherers of short stature in central Africa (Schlicter 1892). The phrase pygmy may refer to the phenotypic trait (Perry & Dominy 2009), for instance referring to both the central African groups and Asian populations such as the Agta and Aeta (Migliano et al. 2007).

Additionally, the term Pygmy may be used as a proper noun referring specifically to the central African groups (Lewis 2000) and this is how it is used in this thesis. There are at least a dozen distinct Pygmy cultural groups inhabiting the forests of Central Africa from Gabon and Cameroon in the west to Uganda and Rwanda at the Eastern extent of the range. Of these the Aka, Cameroonian Baka and the Efe and Mbuti of Democratic Republic of Congo are the most well-known (Bahuchet 2012). These groups are culturally and linguistically diverse, but genetic evidence suggesting a common origin (Verdu et al. 2009, Verdu & Destro-Bisol 2012) supports the use of the collective term.

Pygmies are thought to have a relatively ancient origin, diverging from non-Pygmy populations approximately 60-70 kya. Only the Khoisan show evidence of an earlier point of divergence (Campbell et al. 2014). Diversification of the Pygmy group occurred around 2800 years ago, possibly coinciding with the Bantu expansion through the region (Verdu et al. 2009). Today all Pygmy groups speak languages of the Bantu and Oubangian families (Bahuchet 2012). In this way, Pygmy groups, linguistically, share more in common with their non-Pygmy neighbours than with one another.

The Aka

The Aka language belongs to the C-10 Bantu group (Bahuchet & Guillaume 1982). Whilst closely related to the languages of some surrounding non-Pygmy groups, it is independent, suggesting a long period of divergence since the point of adoption. Today most communication between Mbendjele and non-Pygmies occurs in Lingala, the *lingua franca* of Congo, with a recent origin during the colonial period (Samarin 1991). The precise number of Aka is unknown. Previous estimates have suggested there are between 15,000 – 30,000 people

across both Congo and CAR (Kitanishi 1995). A recent estimate suggests there may be around 100,000 Pygmies of all groups residing in Congo, though this estimate is based on spatial distribution models rather than a census (Olivero et al. 2016). Certainly, the number of Aka living in Congo is in the thousands.

Research on the Aka was scarce until the 1970s onwards. Bahuchet (1985) and a team led by Hewlett (1993) have provided a considerable body of ethnographic and quantitative literature on the Aka of CAR. In Congo research efforts have been hampered by the two civil wars that occurred in the 1990s. Data collected just prior to this period by Lewis, Kitanishi and Takeuchi, however, provide detailed ethnographic information on their subsistence (Kitanishi 1995, 1998, Takeuchi 2005), religious and social practices (Lewis 2002, 2008) . Research on the Aka has been of particular significance in debates regarding the ability of hunter-gatherers to sustain themselves in tropical forests (Bahuchet et al. 1991), the role fathers play in caring for children (Hewlett & Macfarlan 2010) and more recently, social learning (Hewlett et al. 2011).

2.2 Study area

This thesis uses data on three Mbendjele camps located in the Sangha and Likoula departments of Congo. They are situated in close proximity to the town of Pokola. In this section I describe the climate, ecology and recent history of the region.

Climate

The climate of northern Congo, situated close to the equator, Is characterised by high levels of precipitation and mean temperature (figure 2.). The year is divided by two wet seasons, the first from March to June, the second from August to November. The long dry season

(December to March) sees considerable changes to the river levels. This is taken advantage of by the Mbendjele who shift their activities to focus on fishing during this period.

Figure 2.2. Average monthly temperature and rainfall in the Pokola region from 1990 – 2012 (Climate Change Knowledge Portal, World Bank. Data from Climatic Research Unit, University of East Anglia)

Ecology

Rain forest of various types dominates Northern Congo. The study area is characterised by open canopy forest, with a thick understory dominated by plants of the Marantaceae family (Fay 1997). One of these plants, known to the Mbendjele as *ngongo* is of particular significance as a building material and a trade good (photo 1).

The forests of Congo are rich in animal biodiversity. Notably they are home to large populations of elephants (Fay & Agnagna 1991), chimpanzees and gorillas (Poulsen & Clark

2004), as well as large number and diversity of smaller primates, ungulates and birds. Mbendjele typically avoid hunting chimpanzees as there is a taboo against eating their meat. Both chimpanzee and elephant have been hunted and eaten by the Mbendjele in the past. Men especially experienced or talented at elephant hunting were called *tuma*, a term that grants both status and a certain degree of power, though only in this domain (Lewis 2002).

Photo 2.1. Aline, a Mbendjele woman from Masia, carrying *ngongo* leaves that she has harvested from the forest and will sell.

History

The rainforests of Congo provide highly valuable resources in the form of hardwoods such as mahogany. Timber is the second largest contributor to the GDP of Congo after oil (Guiekisse et al. 2014) and much of the forest that is not protected is selectively logged. All three of the Mbendjele camps discussed in this thesis are located within a single logging concession under

the management of Congolaise Industrielle des Bois (CIB), a subsidiary of the multinational OLAM group which acquired CIB in 2011. CIB has forest stewardship council (FSC) certification (FSC 2016) which requires adherence to certain guidelines, designed to ensure that exploitation of timber is performed in a socially and environmentally responsible manner. Given this region's rich biodiversity and in particular the high density of internationally endangered species such as gorilla, conservationists, such as the Wildlife Conservation Society (WCS) have taken a significant interest in this area. The product of the interest in this region from both international business and conservationists is that the Pokola concession has been designated as a conservation buffer zone. Unlike the nearby Ndoki-Noubale national park, hunting is not entirely prohibited in this region but it is under strict control. Eco-guards, partly funded by WCS but employees of the government, are responsible for the policing of anti-poaching legislation. As indigenous people the Mbendjele are given certain hunting rights, but these are restricted to certain areas and techniques.

Along with the Mbendjele the region is home to a number of indigenous Bantu groups who have traditionally practised a fisher/hunter and horticulturalist way of life. As the region has undergone development there has also been an influx of migrants to the area, both Congolese and international.

2.3 The Mbendjele BaYaka

In the following section I provide a brief ethnographic overview of the Mbendjele BaYaka. I cover the structure of their camps, describe their nomadic lifestyle, their economy, social interactions amongst themselves and with other groups and end with an overview of their belief system and rituals.

The Mbendjele refer to camps such as Ibamba, Longa and Masia as *langos*. *Langos* consist of circles of houses, or several such clusters, and sometimes one or more communal structures. Houses typically take the form of *fumas,* small circular structures made by bending branches into a domed lattice which is covered by *Ngongo* leaves. These structures are made by women and can be made so rapidly, with collection of materials and building of the house taking a matter of hours rather than days. Additionally, taller rectangular huts can be found in the camps. These may be made from similar materials to the *fuma* or may have more permanent mud walls. Each *fuma* or hut is the resting place of a single family, usually a married couple and their children. Additionally, small groups of young men who are unmarried or living away from their spouse may reside together in a *fuma*.

In some *langos* a communal structure known as a *mbanjo* will be present, usually located central to a circle of *fumas.* These are usually relatively simple structures, comprising a high wide roof and no walls and are typically constructed by men. Previous ethnographies have described how *mbanjos* were used as a place for men to sleep (Lewis 2002) and dine (Kitanishi 1998). Whilst the former use was not observed in this study we saw some incidents of the latter. *Mbanjos* were not common. They were absent in both Masia and Ibamba. In Longa a structure was built centrally to aid with our data collection and this was adopted by the men as the camp as a social space and appeared to facilitate communal dining (discussed further in chapter 4).

Mobility

The Mbendjele of Ibamba, Longa and Masia are mobile hunter-gatherers. Travelling between *langos* usually as a small family unit, though these may have a fluid structure. It is not unusual

for a husband to leave a camp, perhaps taking one or more of the children, whilst his wife remains with the others. For example, one household which was present in both Longa and Masia, consisted of a young married couple and their one year old baby. Whilst all three were present for the entirety of our study period in Longa the husband left soon after data collection began in Masia. Not long after this the woman and baby also left Masia, travelling to a nearby village where the husband now was. Less than a week later the woman and child returned to the camp but the husband remained in the village. Family units larger than a household often travel together. This coordination is typical between siblings or parents and children but rarer amongst more distant kin.

Reasons for moving camp are many and can be both economic and social. A demand for labour leads many Mbendjele to take up temporary residence in one of the nearby Bantu towns or villages as in the case discussed above. Food Unavailability can trigger large groups to either abandon or move to a certain location. Our second period in the field started just as the dry season was coming to an end. At that point many of the participants from the previous field season were living in a village of 200 + individuals, both Mbendjele and Bantu, gathered to fish and trade. As the dry season ended and fishing became less profitable, the village declined rapidly in popualtion and the Mbendjele made their way to camps better suited to hunting. Social reasons that led to movement in camps included visiting ill relatives, travelling to towns to gain access to healthcare, education or goods such as clothing and avoiding conflict. The Mbendjele are bilocal with a married couple equally likely to live with either the husband's or wife's parents and consequently levels of relatedness are relatively low (Dyble et al. 2015)

Subsistence

Chapter 4 provides a detailed quantitative description of the diet, foraging practices and sharing of the Mbendjele. Here I provide a brief summary of their subsistence. The diet of the Mbendjele in this study comprises a mix of wild plant and animal foods and cultivated carbohydrate staples. Manioc and plantain are sometimes cultivated close to the camps and other times bought from Bantu traders. The predominant economic activity is foraging.

Photo 2.2. Kamba, a Mbendjele woman from Longa prepares a meal of duiker (top) and *fou fou* (bottom). The game was hunted by her father, whilst the manioc flour used to make *fou fou* was bought from Bantu traders.

Groups of women, occasionally accompanied by children and adult men, forage for wild plants in the forests around the camps. Wild yams, nuts and fruits are the most targeted food items but women will often forage for plants that can be sold. Of these non-meat trade goods, *ngongo* and *koko* are the most important. I have previously mentioned how the large n*gongo* leaves are used by Mbendjele when building *fumas* but they are also used in the processing and packaging of manioc. *Koko* (*Gnetum sp.*) is a vine common throughout this region whose leaves are finely cut and used in sauces by both Bantu and Mbendjele.

Male foraging is often targeted at game or honey. Duikers, bush pig (*Potomochoerus larvatus*) and monkeys – most frequently guenons (*Cercopithecus sp.*) – are the most frequently hunted game animals. Additionally small animals such as porcupines (*Atherus africanus*), pangolins and various reptiles are often by products of other foraging efforts. The main means of hunting are with shotgun and snare (photo 3). Spear hunting, net hunting and crossbow hunting are known to the participants in this study but are rarely practised. Several species of honey producing bee are found in the region, I only observed men collecting the honey of honey bees (*Apis mellifera*). As previously mentioned, fish is seasonally important to the Mbendjele. Fishing by the Mbendjele often involved damming a river and then removing the water from the pool so that fish can be collected by hand. Poisons may also be used so that the water does not have to be removed. For a large proportion of the year invertebrates make up an insignificant proportion of the diet. However, for brief periods at certain times of year caterpillars become an important food source as a glut of the insects appear on the large *sapelli* trees (*Entandrophragma cylindricum*).

Photo 2.3. Demonstrating how to build a snare. A loop, usually of wire, but in this case plant material is used, is attached to a bent sapling or branch so that when an animal triggers it it tightens around their leg holding them in place. (photo Nikhil Chaudhary)

Social life and beliefs

The Mbendjele are typically described as egalitarian (Kitanishi 1998, Lewis 2002) in the sense of Woodburn (1982), referring to equality of wealth, power and prestige. In many ways the Mbendjele in this study conform to these first two criteria. Material inequality is low as a result of the lack of any considerable material wealth. Much of their property, for instance baskets, mats and spears, is made by their own hands. Ownership of *fumas* and huts appears temporary. On leaving a camp a family gives up its claim over a house and immigrants to a camp will quickly claim huts that still possess some integrity. That said, certain tools and trade

goods do create material inequality. Notably shotguns are highly desired and ownership comes at both a high material cost and a risks of drawing the attention of eco-guards; consequently gun ownership is rare. Whether this inequality has had any greater social impacts is unclear. In regards to equality of power, the Mbendjele appear highly egalitarian. In most circumstances families are autonomous, making decisions on where to live and how to spend their time and money for themselves. It is in relation to status that a blanket description of the Mbendjele as egalitarian becomes most problematic. Whilst there is no formal hierarchy in Mbendjele society certain senior men are referred to as *kombeti .* Whilst Mbendjele have been found in other research to refer to both men and women as *kombeti* (Lewis 2002), this was not the case during this data collection. The term *kombeti* has previously been translated as elder (Lewis 2002). This suggests that the term is mainly a function of age, but not all old men are referred to as *kombeti.* Instead kombeti seems to be a product both of seniority and status. The *kombeti* often serves as the spokesperson for the camp when dealing with non-Pygmies. As such its occurrence could be seen as a response to the hierarchical structures present in other societies. Whilst the *kombeti* acts as a conduit they do not appear to have any power to sway other camp member's choice. That said, data collected during this study suggests that being a *kombeti*, or of high status more broadly, does beneficially impact on reproductive fitness (Chaudhary et al. 2016). Whether higher fitness is a product or simply a correlate of status remains to be explained, but it is interesting to note that *kombetis* are more likely to have more than one wife than are other men (Chaudhary et al. 2015).

Like many hunter-gatherers, the Mbendjele have a marriage system involving serial monogamy. There is no formal ceremony associated with marriage, but a bride price is paid, either in the form of money or trade goods. Dissolution of marriage shows even less formality,

with couples simply living separately. This in part may explain the relatively high incidence of polygyny in this group. 14.3% of the men in this study are either currently, or have in the past, been married to multiple women at the same time. This is high compared to many hunter-gatherers, but similar to what has been reported for other Aka (Hewlett 1988). Whilst some of these cases may result from the overlap in largely serial monogamous relationships, it is also clear that certain Mbendjele men are able to sustain marriages with multiple women over several years or more.

Both parents are involved in child care though most hands-on care, e.g. washing and feeding, is undertaken by the mother or female carers. Paternal care usually takes the form of keeping an eye on the child whilst the mother is out of camp or otherwise unavailable. The extent and importance of cooperative breeding in this society is hard to assess. Allonursing by both kin and non-kin was observed but infrequent, suggesting it may not have a nutritional purpose but perhaps has social or health related functions. Other forms of allocare were frequent, with kin and non-kin both interacting with children and people of all ages and both sexes taking part.

Mbendjele children are provided with free access to schools in the town of Pokola, and most Mbendjele teenagers and young adults have had some experience at school, acquiring basic literacy, numeracy and exposure to the French language. Attendance at school requires the pupils to reside in the town. As such, the children who participated in the research in this thesis were not at the time attending a school. When a child, or their family, decide they wish to attend a school that child will move to a town, either with a family member or living with relatives already there. It appears that this most frequently occurs during adolescence and this may explain why teenagers are relatively poorly represented in the study population. For the

Mbendjele living in Pokola, attendance at schools is sporadic and not strictly enforced by adults, although many express the opinion that there is value in this type of education. Mbendjele children in the foraging camp spend time both at play and work, participating in domestic and economic activities. A detailed description of how children spend their time can be found in chapter seven.

The Mbendjele have a complex indigenous belief system that, despite the encroachment of Christianity, remains central to their day to day life. A system referred to as *ekila* moderates many aspects of Mbendjele life in particular those involving hunting, consumption of food, menstruation and sex (Lewis 2002, 2008). A man's success at hunting is tied to his *ekila* and his *ekila* is affected by his observance of a wide range of practices. A woman's spouse and male kin cannot hunt while she is menstruating. Almost all Mbendjele have foods which are taboo for them to eat which can be a product of their age, sex or a result of personal experience.

Along with *ekila*, Mbendjele life is shaped by their belief and interaction with *mokondi* (forest spirits). There are many types of *mokondi* which are of significance to the rituals and initiations of the Mbendjele known as *massana*. During a *massana* the whole camp will collect together to sing and dance to the spirits. The woman and girls take the lead with singing, improvising polyphonic songs for extended periods of time, accompanied by simple, improvised percussive instruments. Meanwhile the men and boys of the camp will dance, eventually – depending on the specific *massana* – leading the *mokond*i from the forest, disguised in vegetation or rags to dance with them.

The Mbendjele have a large number of initiation rituals all of which relate to *mokondi.* Rituals are specific to the genders, with women being initiated into *ngoku* (photo 3) and *yele*, whilst

men have a great number of initiations but the most significant and widespread are those of *ejengi* and *balobe*. These initiations represent important rites of passage for the Mbendjele of both gender, but do not occur at a specific age or occasion. Rather the ceremonies take place when circumstances are suitable, though most Mbendjele will have undergone these main initiations by mid-adolescence.

Photo 2.4. The women of Masia singing during a *ngoku* initiation.

Relationships with non-Pygmies

The Mbendjele live in close associations with a number of non-Pygmy groups. Interactions between BaYaka and other indigenous groups, most notably Bantu fishers and hunters, are well documented (Lewis 2002). A perennial question of debate is the extent to which the hunter-gatherer way of life is dependent on their relationship with non-Pygmy groups

(Bahuchet et al. 1991). The Mbendjele refer to Bantu as *Bilo* or, more derogatorily, as *Ebobo,* the Mbendjele word for gorilla. Racism from both sides is clear and animosity frequent, nevertheless cooperation between Mbendjele and Bantu is also common. In two of the sites (Longa and Masia) Bantu also resided in the camp. These were a small number of traders, at most two or three at any given time. They stayed in *fumas*, constructed by the Mbendjele, for a few nights at a time. During this period they would sell food such as manioc flour and palm nuts, as well as cigarettes and alcohol, to the Mbendjele, and provide hunters with shotguns and ammunition. As game is brought to the camp, traders will buy it from the Mbendjele hunters, smoke the meat in order to preserve it. Having collected a sizable load they will travel to one of the nearby market towns where the meat is sold. Several days later the trader will return to the camp and the cycle will begin again.

Mbendjele also provide a source of cheap labour for Bantu agriculturalists and many Mbendjele choose to settle in Bantu villages such as Minganga (Figure 3), although such settlement is often temporary. For those Mbendjele who choose to remain in camps such as Longa and Masia the most interaction with Bantu from the villages involves a degree of coercion to move to the settlements. The Mbendjele are frequently told that their camps are illegal and residents are labelled simply as poachers. The *chef de village* of Minganga would cite discussions he had had with management at CIB when stating that the Mbendjele needed to move to settlements and these same sentiments appear to have filtered through all levels of Bantu society.

Roadside camps such as Ibamba and Longa provide the Mbendjele with a degree of independence not possible in towns and villages such as Pokola or Minganga whilst still

providing them easy access to trade. However, living by the road means that Mbendjele are also forced to interact with eco-guards and employees of CIB. Whilst the latter category includes relationships beneficial to the Mbendjele - CIB provide free healthcare to the Mbendjele and doctors employed by the company make attempts to visit hunter-gatherer camps, though access remains problematic – however, most interaction between the Mbendjele and such bodies are antagonistic mainly as a result of regional conservation policy.

Conservation and the Noubale-Ndoki buffer zone

In 1999 CIB, the Wildlife Conservation Society (WCS) and the Congolese Ministry for the Forest Economy (MEF) signed a protocol which would lead to the creation of the Noubale-Ndoki buffer zone (Elkan et al. 2002), a large area of land surrounding the Noubale-Ndoki national park, itself founded in 1993, which includes villages of the Mbendjele who participated in this study. The stated goal of the buffer zone was to establish "management systems that assure sustainable harvest of legally hunted species so that indigenous people have access to wild meat now and in the future." (WCS retrieved 2017). Unlike inside the national park, where all hunting is prohibited, indigenous groups living inside the buffer zone, such as the Mbendjele, are given hunting rights, but are expected to obey a number of laws. Some laws span the entire buffer zone, such as a prohibition on hunting endangered species and of exporting bushmeat outside of the concession (WCS 2002). Other regulations, particularly those relating to the types of hunting that are allowed, are specific to subdivisions of the region. Monitoring of the buffer zone is the responsibility of ecoguards (WCS 2002). A principle responsibility of the ecoguards, is to man checkpoints on routes through the buffer zone such as the road between Minganga and Pokola, on which two of the study camps were situated (Figure 3). At

checkpoints ecoguards monitor for the export of bushmeat as well as tools used in poaching such as firearms and snares. Ecoguards, on occasion, will visit the Mbendjele villages and consequently the Mbendjele often make sure to hide their shotguns nearby in the forest. Whilst the intentions behind the buffer zone are to be praised, working towards the protection of both wildlife and indigenous populations, in practice the scheme has had a negative impact upon the Mbendjele. I experienced this first hand during my time spent with the people of Longa. This camp is located outside of any of the areas set aside for the Mbendjele and though many of the people there had resided in that area for decades the camp is now deemed illegal. It is a product of a policy that conflates areas of land with particular land use that the people of Longa have now been labelled as elephant poachers, something I was told by Bantu villagers, local administrators and employees of CIB. For those who interact with the Mbendjele on a daily basis the message from the top is clear, to prevent illegal hunting the Mbendjele of camps such as Longa need to settle. This led to aggression between Bantu villagers and the inhabitants of Long and, shortly after I had completed data collection at Longa and moved on to a different camp, the forced eviction of the Longa residents. The Mbendjele's responses to this eviction were twofold, some residents moved to Bantu settlements such as Minganga, whilst others moved away from the road into smaller forest camps, several hours walk from the road.

2.4 Study camps

Figure 2.3. Map of the study area. Major roads which pass by study camps and connect the main towns in the region are highlighted in red. (Google earth 2016)

Ibamba

Ibamba is the most isolated of the three camps. It is in a region of the concession not undergoing current exploitation, on a road with little traffic. On our first visit to this camp we had to stop on several occasions to remove trees from the road, suggesting that it had not recently been travelled. During our data collection period several vehicles passed by over a period of about six weeks. These did not provide trade opportunities for the camps inhabitants,

but tourists on a hunting trip in the region did offer two of the men temporary employment as field assistants.

Ibamba is one of several camps recognised by CIB as a place of residence for the Mbendjele. Whether because of this fact or its relative isolation, the residents of this camp received no pressure to move elsewhere. Large manioc fields surround the camp as well as a decent number of plantain and other fruit trees, and these cultivated foods comprised the core diet of the residents.

Ibamba consisted of 45 people in 13 households (table 1), 24 adults and 21 children (< 18 years). Unlike the other camps, it was not clearly clustered. Instead the households were spread out over a large clearing.

Longa

Longa is the largest of the three camps and comprised a number of distinct clusters situated along the road. In total, Longa comprised approximately 18- 20 households. Each cluster often comprised a particular family group. Analysis in this thesis focusses on the largest cluster within Longa which consisted of 39 people in 11 households (table 2), 20 adults and 19 children (< 18 years). Longa is situated on a busy road between Pokola and the Bantu village of Minganga (figure 3.) Whilst the road by Ibamba saw several vehicles a month, that past Longa and Masia saw several vehicles a day. Many of these vehicles carried traders using the roads to transport game from the forests to the towns. Like Ibamba Longa was surrounded by fields of manioc with a large number of fruit trees nearby.

Masia

Masia was the smallest of the camps, comprising 30 people in 8 households (table 3), 15 adults and 15 children. The camp formed two clusters with approximately 100 metres separating them. The households were not evenly distributed across clusters, all but two (households 4 and 7) were situated in the larger cluster. Masia is situated close to Longa on the same busy road (Figure 3.). However, unlike both Longa and Ibamba there were no gardens or fields in the surrounding area. Consequently, cultivated foods could only be accessed through trade.

Summary

For a number of reasons, the Mbendjele of the Pokola/Minganga region provide an excellent research focus. In their continued focus on foraging and their highly mobile way of life they provide an increasingly rare opportunity to study the ecology of this form of subsistence. That is not to say that therefore this population is a perfect model for all hunter-gatherers throughout human history. Indeed, a strength of this population to researchers is that it offers an opportunity to understand the considerable differences in behaviour of foraging people exposed to different ecological factors. In particular, it provides ample opportunity to study the impact of market integration and other related factors on the Mbendjele and their foraging economy. By comparing a relatively isolated camp such as Ibamba to the more integrated Longa and Masia we can begin to identify the ecological conditions under which behaviours such as food sharing are favoured. Furthermore, the difference in social structure of the camp, i.e. the population size and degree of relatedness in the camps, provide an opportunity to examine the impact of social structure upon cooperation and social learning.

Table 2.1. Household composition – Ibamba. Households are defined by the author as those individuals who pool their production

Household	adult males	adult females	male children	female children	household size
1	1	2	2	1	6
2	0	1	1	1	3
3	1	1	3	1	6
4	1	1	2	1	5
5	0	1	0	0	1
6	0	2	1	0	3
7	1	1	3	1	6
8	0	1	0	0	1
9	1	1	0	2	4
10	1	1	1	0	3
11	0	1	0	0	1
12	1	2	0	0	3
13	1	1	1	0	3

Table 2. Household composition - Longa

Household	adult males	adult females	male children	female children	household size
1	0	1	1	0	2
2	1	1	2	1	5
3	0	1	0	0	1
4	1	1	2	1	5
5	1	1	0	0	2
6	1	1	1	0	3
7	1	1	0	0	2
8	1	2	3	2	8
9	1	1	3	2	7
10	0	1	0	0	1
11	1	1	1	0	3

Table 3. Household composition - Masia

Household	adult males	adult females	male children	female children	household size
1	0	1	1	1	3
2	0	1	2	0	3
3	1	1	1	1	4
4	1	1	1	0	3
5	1	1	1	1	4
6	1	2	1	1	5
7	1	1	0	0	2
8	1	1	1	3	6

3. Data collection

Data collection occurred over two field seasons; April – June 2013 and March – July 2014. The first season was used to search for potential participants and field assistants, the collection of preliminary genealogical, anthropometric and age data and to inform study design and questions for the following season.

3.1 First season

The first season was undertaken by five researchers; James Thompson (the author), two other PhD students from UCL anthropology Nikhil Chaudhary, Deniz Salali and two post-doctoral researchers Pascale Gerbault (UCL Genetics) and Jed Stevenson (UCL Anthropolgy). On arriving in Pokola initial efforts went into identifying potential field assistants and study sites. In both of these endeavours we were greatly aided by Jerome and Ingrid Lewis who have worked with the Mbendjele since Jerome began his own PhD research in 1994 (Lewis 2002).

Field assistants

Given the nature of the relationship between Bantu and Pygmies we sought Mbendjele field assistants to aid with our work. This had many benefits; interviews could be conducted in Mbendjele rather than Lingala, the experiences of our field assistants were able to inform our understanding of the Mbendjele and the direction of our research and they greatly aided our integration with the study participants. Whilst the number of Mbendjele who speak French is considerably smaller than Bantu we were fortunate enough to find and hire Mekouno Paul, Esimba and Dambo and gain the temporary assistance of Independent, a Mbendjele employee of CIB with excellent French who aided in training the other field assistants.

The main role of the field assistants was to serve as translators. To ensure a high degree of accuracy we staged mock interviews between the field assistants for each of the protocols and had assistants back translate questionnaires previously translated by the other assistants.

Photo 3.1. Research team during first season. From left (front row) Independent, Nik, Deniz, Paul, Dambo, (Standing) James, Pascale, Jerome, Esimba, Jed. (photo: Jed Stevenson)

Locating study sites

The route between Pokola and Minganga was chosen as the initial area of study as the road allowed for easy transport for our large team and considerable amount of equipment. Furthermore, we were aware there were several Mbendjele camps in this area. The initial plan was to use these roadside camps as a base of operations travelling for shorter periods of time to remoter camps further from the road. However, it became clear, as discussed in chapter 1,

that most Mbendjele in this region chose to live by the roads for the majority of the year. This provided us the opportunity to study the effects of market integration on the Mbendjele. During the first field season we worked in three camps along the Pokola-Minganga route; Longa, Enoko and Mbaya.

During our time in the camps our research team stayed adjacent to the Mbendjele camps. This ensured we were close enough to engage in data collection throughout the day, whilst also providing us with a separate space where we could work in private, for instance when we were performing interviews or games that required anonymity. However by staying close to the camps it meant, not only that we had ease of access, but that we could interact and socialise with the Mbendjele outside of research hours and in doing so gain greater insight into the Mbendjele and facilitate further research.

Consent and Compensation

Consent of the participants was asked at various stages of data collection. On first arriving at a camp we introduced the research team and provided an overview of our work. At this point we ensured that as a group they were willing to let us stay in their camp. Subsequent to this we provided a more detailed explanation of our research, how and what data we would collect and what we would use this data for. To aid in this explanation we constructed small posters as visual guides. These were of particular use in explaining certain concepts and practices such as the collection and analysis of genetic data. Prior to data collection we then asked each individual for consent in written form. Whilst the written consent form covered all data collection, participants were free to stop participating at any time and we sought informal spoken consent for each type of data collection.

Participants were compensated in a number of ways. Most data collection was compensated with food, usually rice, palm oil and salt. Additionally, each household which participated in the mote study (described below) were given a machete or cooking pan.

3.2 Second field season

The second field season was undertaken by James Thompson, Nikhil Chaudhary, Deniz Salali, Pascale Gerbault and Aude Rey, an MSc student at UCL Anthropology. Mekouno and Dambo returned as field assistants and were joined by Guyfano and Nicolas. During this period we resided in and collected data on three camps. Longa, Ibamba and Masia. Two of the camps we had previously visited (Enoko and Mbaya) were empty. Whilst we had worked with some of the participants previously, many were new. Longa and Masia were chosen as study populations as we already had data on these camps from the previous season. Whilst we had not previously visited Masia it is located on the same route as the camps visited in the first trip. Consequently, many members of this camp already appeared in our data set, either as prior informants or relatives thereof. Ibamba was chosen as an additional study site as the lower degree of market integration, a consequence of its location on a rarely travelled route several hours drive from the nearest village, provided an informative contrast to the well-integrated Longa and Masia.

3.3 Contributions to the research

The research in this thesis was undertaken as part of a larger project on hunter-gatherer resilience, funded by the Leverhulme trust. As such the thesis has benefited from cooperative data collection and data sharing as well as drawing upon the expertise of other team members. Those responsible for the collection of data are as follows

- Mbendjele genealogical data: James Thompson, Nik Chaudary, Deniz Salali, Pascale Gerbault, Jed Stevenson and Aude Rey.
- Mbendjele ageing data: James Thompson, Nik Chaudary, Deniz Salali, Pascale Gerbault, Jed Stevenson and Aude Rey.
- Mbendjele motes data: James Thompson, Nik Chaudary, Deniz Salali and Aude Rey.
- Agta genealogical data: Mark Dyble, Wallace Hobbes, Andrea Migliano, Abigail Page and Dan Smith.
- Agta ageing data: Mark Dyble, Wallace Hobbes, Andrea Migliano, Abigail Page and Dan Smith.
- Agta motes data: Mark Dyble, Wallace Hobbes, Andrea Migliano, Abigail Page and Dan Smith.

All other data reported in this thesis was collected solely by myself.

Several sets of data, namely genealogical and aging data, were managed cooperatively by the resilience research team and the analysis of the ageing data was performed by a team headed by Mark Thomas and Yoan Diekman. All other analyses are my own work.

3.2 Data collection protocols

Glossary of terms

Throughout the thesis several terms are used to refer to specific structures and units on analyses. Whenever theses terms are used, unless stated otherwise, they refer to the following features.

Household: When using the term household I am referring to an economic unit of Mbendjele who pool all their productivity together. I divide each camp into a number of households so that all individuals in the camp are a member of one household and no more than one household. This division is based upon whether individuals typically cook and eat together. Often this corresponds to those individuals sharing a *fuma* or hut, but on occasion multiple households may live in a single structure. Often a household will be comprised of a husband and wife and their children but other household structures occur and the term household, as used herein, does not imply any degree of kinship between individuals within a household.

Meal: A meal is defined as an event at which one or more individuals consumes food. This may be cooked food or simply items such as fruit and bread which are consumed without any preparation. I label an individual's share of a meal a portion thus a single meal consists of multiple portions of food.

Food sharing: Any transfer of food between two households (as defined above).

Meal sharing: Specific cases of food sharing where the food transferred between households consists of one or more portions of a meal (as defined above).

Adult: Individuals of 18 years and older.

Children: terms such as child, juvenile and adolescent obey common usage in the main text. However, in regards to analysis, children are individuals less than 18 years old. Where finer subdivision of age categories were used in analyses these are described in the relevant results section.

<u>Sampling</u>

Data collection required sampling of the Mbendjele population at multiple levels. At higher levels, i.e. the choice of which camps to study, sampling was non-random. The Pokola/Minganga region was chosen for logistical reasons and for the added benefit that Jerome Lewis had previously worked in the area. The camps in this area were chosen as they provided a large sample of individuals present in both field seasons. In the first incidence, Longa was chosen as a sample camp as they provided a large sample of individuals and it was easily accessible from Pokola. As it was also inhabited during the second trip, with several of the families still present, it became a focus of the research. Both Masia and Ibamba were chosen to provide an ecological contrast to both Longa and each other. Masia was chosen due to the high productivity of hunters, whilst Ibamba was chosen as a relatively isolated camp. This non-random sampling clearly limits the uses and interpretation of data reported in this thesis. For instance, it would be inappropriate to estimate levels of bush meat offtake by hunter-gatherers in this region without a better understanding of which, if any, of the camps was representative of other groups. On a related note, all data collection occurred within a relatively brief period. The Mbendjele's way of life, particularly their economy, is tied closely to the changing seasons and this thesis is not able to account for that. Thus, all results should be interpreted within the specific ecological conditions under which the data was collected, hence the value of specifically choosing three camps with differing ecologies.

Within camps, every effort was made to sample all individuals in a systematic manner. For example, the order of focal observations was randomised whilst ensuring even coverage across hours of the day and days of the week. In all of the camps it was not possible to sample all individuals for practical reasons. In Longa the large size and structure of the camp, which could better be described as an aggregation of several camps along a stretch of road, precluded

certain types of data collection on all individuals. It was simply not possible to observe all households. In this case the largest of the subcamps was chosen as a research focus. In both Masia and Ibamba all households within the camp were included in the study. Having selected the focal camps, the goal was to collect data on 100% of households within those camps and 100% of individuals within those households, thus, no sampling occurred at these lower levels. Nevertheless, the data set is incomplete due to either households choosing not to participate or moving away during critical periods of data collection. Furthermore, accidental data loss, for example, resulting from a malfunctioning sensor, also occurred and in these cases certain individuals or households were excluded from the analysis. Such data loss is unfortunate but unavoidable. In many cases such losses are fairly random and thus should not disrupt results to too great an extent. However, individuals choosing not to participate or moving away is less random and could well insert biases into the data and this needs to be borne in mind.

Genealogical information

Genealogies were constructed based on interviews with all adults in Longa (both seasons), Enoko and Mbaya (first season), Masia and Ibamba (second season). Interviews were conducted in Mbendjele via native speakers. Participants were asked the following questions in regard to themselves, their parents and their grandparents.

- Names of all spouses.
- Names of all offspring, their sex and order of birth.
- Whether these named individuals were living or deceased.
- Where deceased, participants were asked for the cause of death and the life stage (e.g. baby, child, adult) at which they passed away.

This information was recorded as hand drawn genealogies (photo 2). Each individual who appeared in a genealogy was given a unique ID number. Since there is substantial cross over between the genealogies of different participants this required cross referencing which was performed in the field. This allowed any queries regarding the identification to be addressed to participants. Subsequently a database was constructed with important genealogical information for each individual. This dataset comprised information on 2890 individuals of whom 673 were participants (i.e. were present in the camps at some point during data collection). The remaining 2217 were absentees. For each individual (participants and absentees) the ID of both parents were noted. Using these data, we were able to construct a population wide genealogy using the pedigree package in R (Coster 2015). From this we were then able to calculate coefficients of relatedness for any given dyad in the population.

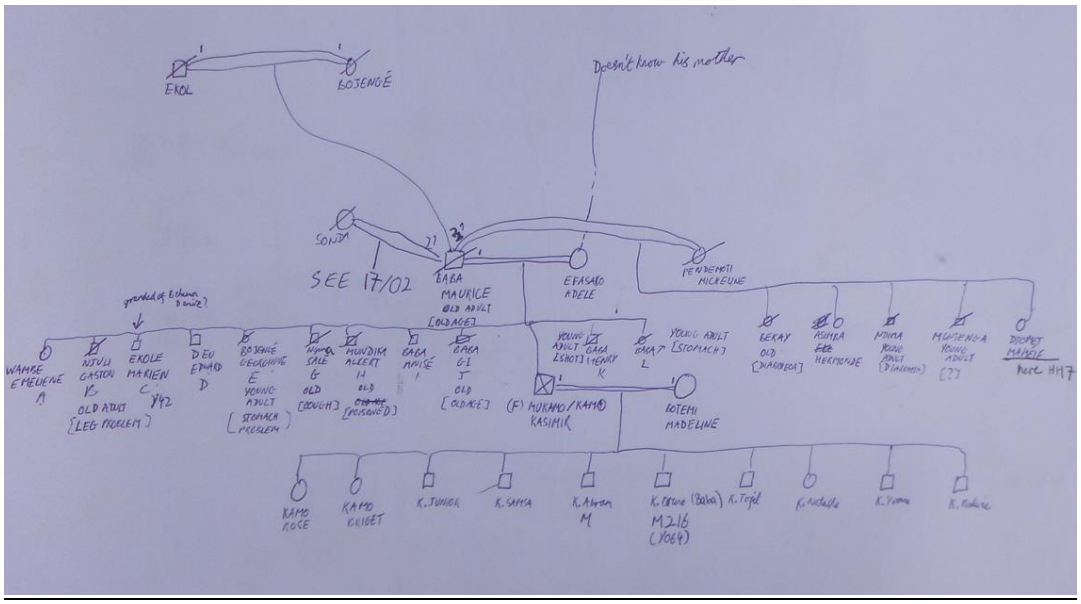

Photo 3.2. An example of the genealogies collected. Ego (Mukamo Kasmir) is denoted by the central square with a cross. Squares denote males, circles females. Diagonal slashes denote where a person is

deceased. Single lines denote offspring, double horizontal lines denote marriage. Names, cause and life stage at death and birth order (using letters A,B,C ….) are recorded beneath the shapes.

Anthropometrics

Anthropometric data and saliva samples were collected for all participants during the same period as genealogical data. With the exception of dental data, this information was not used in this thesis thus these protocols are not reported here.

Dental data

For all children the number and position of their teeth was recorded. Via reference to a chart (Appendix 3.A), this was used to ascribe a broad age category which was used in the ageing methods detailed below.

Ageing

The process of ageing the participants involved three steps - the construction of a relative age ranking, assignment of initial age estimates and calculation of final estimates using Markov chain Monte Carlo methods.

Relative age ranking

In each camp the participants were asked to collectively construct an age ranking. To do this we used Polaroid photos of all participants. First the photos were divided into loose age cohorts by the researchers. These roughly corresponded to individuals less than 1 year, 1-1.9, 2-4.9, 5-9.9, 10-14.9, 15-19.9, 20-24.9, 25-29.9, 30-39.9, 40-59.9 and 60+. We then asked as many camp members who were present and willing to participate to gather in a central location where we presented them with the photos, asking them to place them in order from

youngest to eldest for each cohort (photo 3). Photos were presented one at a time and the participants were first asked to name the individual. This ensured they knew the person and were ageing based on their knowledge of them rather than their appearance. Almost all individuals could be identified, but in the few exceptions where the photo could not be identified that individual was excluded from that particular ranking. Following identification of the photo, participants were then asked to place the photo relative to others, forming a line from youngest in the cohort to the left and oldest to the right. Where there was disagreement we left the participants to come to a consensus, simply stating we required a single answer from the group. After two consecutive cohorts had been ranked, the oldest ranked individuals of one cohort were ranked compared the youngest of the following cohort in order to produce a reliable ranking at cohort boundaries.

Across the study period four separate age rankings were constructed, three for participants in the Minganga region (Longa, Masia, Enoko and Mbaya) and one for Ibamba. Age rankings were calculated separately for Minganga and Ibamba as these represent two distinct populations with very little cross over. In contrast, members of the four camps in the Minganga region were well known to one another. The Ibamba age ranking was constructed in the second field season. Two of Minganga rankings were made in the first season in Mbaya and Longa respectively.

Since there was little overlap between the social networks of Ibamba and the other sites separate age rankings were constructed for the Minganga camps (Longa, Masia, Enoko and Mbaya) and Ibamba. The number of participants in the first season represents only a

subsample of the total participants from Minganga. As such a third age ranking for this region was constructed in the second season including participants from both seasons.

Assignment of age estimates

To anchor the age ranking we asked for particular events that we could precisely date and that the participants could link to the birth of specific individuals. The construction of the road between Pokola and Minganga (chapter 2, figure 3.) could be dated to 1997 and we were able to identify a number of people born in this year. Additionally young children born immediately prior to the data collection, or in the period between the two field seasons were used as anchors. For the large majority of participants no concrete anchor point was known. For these people an age estimate, giving a lower and upper bound, was provided by researchers, making use of data on dental development, birth order and appearance.

Calculation of final estimate

Age rankings and estimates were then used to provide a more precise estimate of age. This was calculated using a new method developed by Prof. Mark Thomas and Dr Yoan Diekman of UCL genetics. A Gibbs sampling framework was used to derive a probability density distribution using both the relative age list and preliminary estimates. A mean age for each individual was then estimated by collapsing the distributions to produce point estimates. Full details can be found in Diekman et al. (2017).

Photo 3.3. Nik and Dambo creating a relative age ranking with the people of Mbaya. Polaroid photos of the participants are being placed in order of youngest to oldest based on group consensus. (Photo: Deniz Salai)

Activity Budgets

Scan sampling was used to construct activity budgets for camp members. During a scan all the individuals in the camp at the time were recorded, along with their activity at the time. Additionally, it was noted who was in close proximity (roughly 5 metres) to one another and the identities of people participating in activity together were recorded. This includes both people cooperating in a task, for instance women preparing a meal together, but also child care. Scans were scheduled evenly throughout the day between 6:00 and 18:00 and performed

on the hour. In Ibamba and Masia scans were performed hourly. This allowed us to estimate the length of time spent out of camp on foraging trips, which appears as consecutive absences in the scan data set. Scans in Longa where performed in the same manner except that scans were not performed every hour, as such consecutive absences are not recorded for this camp.

Activities were categorised as

- Resting: standing (no activity), sitting (no activity), sleeping.
- Subsistence (in all cases the type of food was noted): cooking, processing plant (food), processing meat, foraging, sharing, eating.
- Domestic: cleaning, collecting fire wood, collecting water.
- Childcare: breastfeeding, holding child, washing child, feeding child.
- Manufacture: making tool, making basket/mat, processing plant (non-food), constructing building, maintaining tool.
- Social: talking, playing, grooming, trading, singing.
- Other: walking (no activity), personal hygiene.

It should be noted that play is a broad category, inclusive of a range of activities such as competitive games, work imitation and social play. Often it is the case that a child's behaviour coulod be described both as play and another behaviour, for instance, foraging. In these cases the decision on which category to place the behaviour was decided upon by the apparent result. For example, children foraging for fruit around the camp was recorded as foraging if the food was subsequently eaten. Whereas, in those cases where food such as unripe papaya where harvested and then not eaten, but rather thrown about the camp, this was recorded as play.

Many of these activities are not mutually exclusive. For instance, two women may be together talking. In addition, one is constructing a basket whilst the other breast feeds. In these cases, multiple activities were recorded and for each activity a separate group coded. The above example would be coded as follows.

Woman 1 - talking (activity group 1), constructing basket (0), [proximity group 1]

Woman 2 - talking (activity group 1), breastfeeding (activity group 2), [proximity group 1]

Child 1- nursing (activity group 2), [proximity group 1]

In chapter 7 I compare activity budgets of Mbendjele hunter-gatherers with those of the Agta fisher-gatherers from the Philippines. These data were collected by Mark Dyble, Abigail Page, Daniel Smith and Andrea Migliano: members of the hunter-gatherer resilience project at UCL. Methods used were the same as those for the Mbendjele with a couple of notable exceptions. Scans were performed less regularly but over a longer period. Data on people absent from camp were collected during the scan by asking camp members who were present where absentees were and what activity they were engaging in. Data on frequency and length of out of camp activities were constructed from this.

Household focal observation

Systematic observations were used to record production, consumption and sharing events in camp. Systematic observation occurred between 06:00 and 18:00, corresponding with the hours of daylight in the region. Camps were divided into household clusters. Each cluster was approximately 3 – 5 households that could be easily observed simultaneously. An observation period lasted 2 hours. During this time, any consumption, production or sharing event in the

focal cluster was recorded. Each cluster was observed for a total of 24 hours (Longa) or 36 hours (Ibamba and Masia). Observation periods were evenly spaced throughout the day so that each cluster was observed between 06:00 and 8:00 twice (Longa), or three times (Ibamba & Masia). Focal clusters were rotated so that the same cluster was never observed during two consecutive observation periods. Observation occurred over several days to account for changes in conditions. Events were recorded in the following manner.

Production

Any members of the focal households (those households within the specific cluster) who returned to camp with food were recorded. Animals were weighed individually and identified. The total amount of plants returned was weighed and the different types identified. Non-foraged foods, such as rice or bread, brought into the cluster were recorded in the same manner. In total 214 production events were recorded, of which the large majority were of plant foods and cultigens (table 1). Except in Masia, no meat was brought into focal clusters during observation. Thus, estimates of hunting productivity in Ibamba and Longa are based on *ad libitum* sampling. Any time meat was brought into the camps during our time there this was recorded in the same manner as during the focal observation. As hunting productivity was low in these camps, it was possible to keep track of total productivity in this way.

Consumption

Consumption of food, irrespective whether the consumer were a member of the focal household, was recorded as a consumption event. The ID of the consumer, the food they were eating and a visual estimate of the amount consumed were all recorded. The source of the

food was recorded as the household of the consumer except where a prior transfer had been recorded (see “sharing” below).

Where multiple people were involved in a consumption event, for instance multiple people eating from the same plate or sharing a piece of fruit, all individuals were assumed to take an equal share, as estimating separate consumption values would be impractical.

Any cooking or processing of food in the cluster was recorded. The quantity and types of food used were noted as were the IDs of any people involved. A total of 2030 consumption events comprising 702 meals were observed across the three sites (table 1).

Sharing

Food sharing was recorded in two ways:

Resource sharing was recorded at the same time as production events. We also captured sharing outside osystematic observation. When a person returned with food we recorded the ID of anybody outside of the resources holder’s household who received a share. The quantity, type and part of the food they received were recorded.

Meal sharing was recorded during focal cluster observation. Any food from the focal households given to somebody outside the household to consume was recorded. The amount and type of food were recorded as a consumption event. When cooked food was transferred outside of the cluster to be consumed elsewhere, the recipient household was recorded but this was not counted as a consumption event.

For all the above cases, quantity of food was recorded. For raw resources, this took the form of weight with meat or number with foods such as plantain. Meat was weighed using a spring

scale at the point it was brought into the focal cluster. For meals, if the cooking process had been observed, count estimates of raw resources were used to estimate total meal quantity. Where this was not available, quantity was estimated based on the receptacles used to cook and/or serve the meal. Counts of food items were subsequently converted into mass using a mean weight calculated from several of the food items. Where items showed clear variance in size, for instance with yams and plantain, items were categorised as small, medium and large and separate means used for each category. Weight estimates were converted into calorific values based on previously published data (Appendix 3.A). The estimates of weight, and thus also calorific values, are imprecise. As such, the data reported in this thesis cannot be used to give a detailed account of the diet of the Mbendjele. Nevertheless, I believe the somewhat crude measure still provides suitable data to compare food sharing between different households.

Table 3.1. Count of production and consumption events recorded during systematic observation.

	Production				Consumption	
Camp	total events	wild plant	cultigen	meat	total events	meals
Ibamba	76	32	49	0	840	286
Masia	69	39	13	13	774	252
Longa	69	36	26	0	416	164
total	214	107	88	13	2030	702

Proximity data

Proximity data were recorded using “motes” a portable wireless sensor, measuring 50mm*35mm*15mm. The motes used were custom modifications of the UCMote Mini (Unicomp) and used a modified TinyOS operating system developed by Wallace Hobbes. Motes

send out unique radio signals (beacons) at a specified time interval, whilst also recording any beacons it detects within a given area. Thus, motes can be used to produce a proximity network in much the same way that observational scan data are used, but at a far greater resolution.

Motes were used to construct proximity networks in all three camps. In Longa and Masia the motes experiment lasted seven days. In Ibamba the experiment lasted nine days. Prior to the start of the experiment each mote was fully charged, the memory wiped and the software programme installed. The motes were then turned on and specific time that each individual mote was turned on was recorded. This is necessary to convert the motes' arbitrary measure of time to real world time (discussed in more detail below). The motes were then wrapped in several layers of Clingfilm for waterproofing and placed in belts which could be worn round the waist of adults or across the chest, for small children. Each individual in the camp (adults and children) were given a mote and belt and the unique id of the mote each person received was recorded. The time at which the last person in camp received their mote was recorded as the start of the experiment. If new individuals entered the camp during this period, they were promptly given a mote and the time recorded. Similarly, if people left the camp during the period the motes were returned and the time recorded. Participants were asked to wear their mote at all times, and researchers and field assistants also wore motes throughout the experiment period. At the end of the experiment all motes were collected and the id's checked to identify any cases where motes had been swapped. Where motes had been swapped during the study period the data for both individuals involved were excluded from analyses.

The motes were set to send a beacon every 2 minutes and record all beacons from motes within 3 metres. Motes recorded data 24 hours a day. However, data from overnight (20:00 – 05:00) were subsequently excluded from analyses. On detecting a beacon a mote records the id of the sender, the strength of the signal – which varies with the proximity of the two motes to one another - and a time stamp detailing the time (in milliseconds) between the point the receiving mote was turned on and when it received the signal. Thus at the end of the experiment each mote contained a large data file with many such records. For each camp this data was converted into a matrix where each column/row was an individual and each cell provided the count of beacons recorded for that particular dyad. We then constructed a second matrix with the count of potential beacons a dyad could have recorded. This is simply the total amount of time ego and alter were simultaneously participating in the experiment divided into two minute intervals. Then by dividing the actual beacon count by the maximum possible count we were able to calculate the proportion of time ego and alter spent within 3 metres of one another. These proportional data could then be used to construct proximity networks, whilst allowing for the different length of time people participated in the experiment.

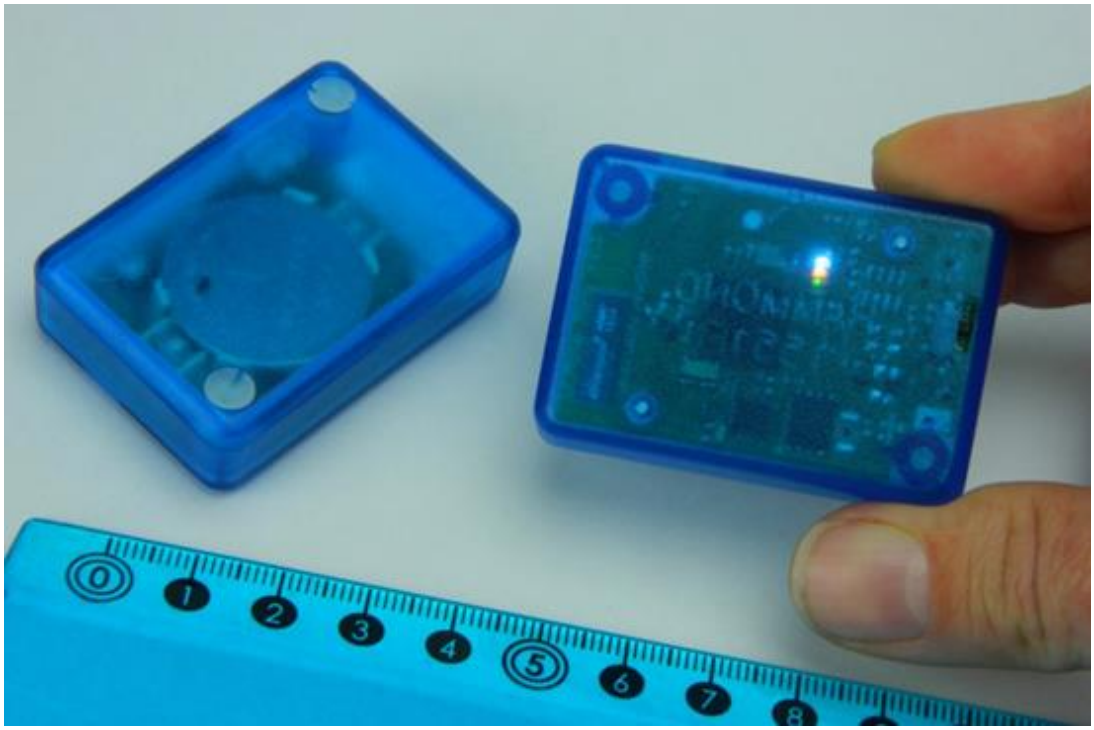

Photo 3.4. The UCMote Mini (Photo - Wallace Hobbes)

4. Impact of market integration on the foraging niche of the Mbendjele.

An important consequence of a focus on high quality but hard to acquire foods is a high degree of variance in the productivity of human foragers. This variance has been used to explain the widespread occurrence of food sharing in immediate return societies. Access to modern technologies, cultivated foods and trade can all reduce the levels of variance. Thus, we predict they would also lead to a decrease in sharing. In this chapter I test this hypothesis and assess the impact of factors related to market integration on the subsistence of the Mbendjele. Comparisons are between three contemporary camps with varying degrees of market access and horticultural practice and previously published ethnographic data on Aka subsistence which was collected prior to the recent and rapid development of the region. The economy of the contemporary Mbendjele differs markedly from the "traditional" view of hunter-gatherers. Nevertheless, foraging remains the primary economic activity of the Mbendjele. Food sharing does not show a simple decline with market integration, rather, different types of sharing are affected by different integration factors. The sharing of meat is comparatively rare in this study population, a consequence of an absence of large scale cooperative hunting and participation in the bush meat trade, in contrast, meal sharing remains prevalent. These results are of significance in regards to our understanding of the ultimate and proximate explanations of food sharing. Additionally, by exploring variation in subsistence both between groups and over time the results herein are of consequence to the applicability of hunter-gatherer studies to the human evolution literature.

4.1 Introduction

Despite comprising a small proportion of the global population, foraging people have had a disproportionate impact upon our understanding of human evolution, particularly in the field of human behavioural ecology (Nettle et al. 2013). The prominence and status of this research are clearly based on the assumption that hunter-gatherers provide unique insight into our pre-agricultural past. The suitability of modern hunter-gatherers as a model for pre-agricultural hominins has received significant criticism, with even sympathetic reviews cautioning that the impact of technology needs to be accounted for (Marlowe 2005). Whilst contemporary hunter-gatherers cannot be assumed to be perfect models for pre-agricultural populations, undoubtedly, they provide insight into the unique selection pressures which affect foraging populations. Unfortunately, recent centuries have seen a rapid decline in the number of hunter-gatherers. The Agta of Casiguran underwent dramatic population decline between 1962-1986 (Headland 1989), and the process and effects of sedentarisation are well documented for the Ache (Hawkes et al. 1987), Baka (Kitanishi 2003) and Agta (Page et al. 2016). Any study of contemporary hunter-gatherers is inevitably an examination of the influence of external pressures on these groups and, to a greater or lesser extent, descriptions of a population under transition. Understanding processes such as sedentarisation and the impact of market integration is invaluable. In practical terms, it can inform land management, health and education policy. From a scientific perspective, studies of populations under transition can provide insight into not only our pre-agricultural past but also periods of change such as the Neolithic agricultural Revolution.

In this chapter, I consider the impact of market integration on our study population, specifically comparing their diet and economic practices to previously published accounts

of Mbendjele subsistence. This provides an important baseline for the rest of the thesis. I address the question of whether the social foraging niche, outlined in chapter 1, serves as a valid description of contemporary hunter-gatherers and thus appraise their usefulness as an evolutionary model. Additionally a detailed quantitative description of the Mbendjele diet, foraging and sharing practices can assist understanding of subsequent analyses. In particular, this chapter provides a detailed comparison of food sharing by Mbendjele in the past and present. This is of significance as food sharing is a behaviour often over simplified in the literature, and theoretically should be highly sensitive to changes related to market integration.

The impact on food sharing

Food sharing is a well-studied aspect of hunter-gatherer behaviour. As an overt and easily measurable form of cooperation between individuals across the full spectrum of relatedness found in hunter-gatherer bands, it has proven a profitable focus of work on cooperation in humans. In contrast to humans, food transfers by other primates rarely occur between non-kin (Mc Grew 1975) A range of theories have been suggested to explain why food sharing is ubiquitous in forager societies, most notably kin selection, reciprocal altruism and tolerated theft. In chapter 5 these theories are discussed in detail and their relevance to sharing amongst the Mbendjele appraised. This chapter instead what is common between these theories. That is to say, underlying all such theories is the basic hypothesis that transfers of resources should occur when the relative value of the held resource is lower than its value to other group members. Such preconditions are common in immediate return societies due to two factors, high variance in short-term productivity and steeply diminishing returns with increasing amounts of food.

In chapter 1, I described the hunter-gatherer foraging niche as one targeting difficult to acquire foods and that one of the factors which contributed to this difficulty was an uneven temporospatial distribution. Hunting can involve considerable investments of time before the prey item is even encountered and many trips end with the hunter returning empty handed. Amongst the Hadza a single hunter could be expected to catch a large game animal in only 1 of 37-53 days, depending on the season (Hawkes et al. 1991). Once encountered and successfully caught, game can provide a glut of resources. The most common prey of the Mbendjele, duikers, weigh between 3 and 15 kilograms depending on the species. Larger animals such as bush pigs, gorillas and elephants dwarf this figure. The end result of low encounter rates and large package size is high variance in resource holdings between hunters. On any given day it is likely that some households will have large amounts of meat whilst others have none.

Inequalities in resources holdings are of course not unique to hunter-gatherers, in fact quite the opposite. Measures of material inequality amongst hunter-gatherers are typically low, with one study on a number of hunter-gatherer societies reporting an average |Gini coefficient of 0.22 (Smith et al. 2010), in comparison, an average calculated from a number of pastoralist societies was 0.51 (Borgerhoff Mulder et al. 2010). Gini coefficients provided a measure of dispersion of wealth and typically range from 0 (highly equal) to 1 (highly unequal). Hunter-gatherers have relatively low levels of material inequality, thus variance in resource holdings alone is not enough to explain why sharing is so frequent in forager societies. It is only when this is combined with diminishing returns in the value of resource holdings that variance in productivity translates to variance in value. In the absence of storage, linear increases in resource amount have diminishing marginal returns in terms of fitness. However, for other camp mates with little or no resource holdings they possess

relatively high value. Thus, sharing amongst hunter-gatherers is a product of high variance in resource holdings, resulting from a focus on large packet size, unevenly distributed resources and diminishing marginal value, resulting from the absence of long term storage. It is the latter of these two traits which explains the wide spread occurrence of sharing amongst foragers. Neither pastoralist nor agrarian systems not subject to the same diminishing values. Grains can be stored for long periods with relative reliability, and livestock can be harvested when there is need. Even under these conditions fitness value will not increase linearly with increasing resource holdings as a consequence of various risk factors, but the diminishing returns are far smaller. Consequently, in these societies it pays to accumulate wealth rather than transfer it, be that for inclusive fitness, reciprocal altruism or tolerated theft.

The logical extension of this is that, if either reduction in variance of productivity and resource holdings or changes to the value curve towards a more linear relationship with quantity were to arise, we would expect a decline in sharing. The Mbendjele provide an opportunity to test this prediction, as development and shifts in the demography of that region have impacted on their way of life.

To understand the impact of market integration on food sharing it is necessary to first describe sharing in the absence of market forces. Kitanishi (1998) describes the sharing practices of a Mbendjele group during a period of several months when they were living in the forest and not actively participating in trade. During this time, all food they found and hunted was eaten in the camp and they had limited access to cultigens. Under these conditions the Mbendjele exhibit a multi-tiered system of sharing. Meat underwent two distributions prior to cooking. These will be referred to as the primary and secondary distributions. Then after the food was cooked it underwent a third and final distribution,

henceforth meal sharing. In this way sharing by the Mbendjele resembles that of other Central African Pygmies (Bahuchet 1983).

The primary distribution follows specific rules, with certain parts of animals given to people depending on the role they played in its acquisition. For example, the head of a bush pig caught during a spear hunt is given to the owner of the spear that dealt the third blow, the dorsal midriff is given to the owner of the spear that dealt the second blow and the owner of the spear that dealt the first blow takes all other parts (Kitanishi 1998). Given these rules, it is not surprising that Kitanishi reports that men rarely hunt with borrowed spears.

The secondary distribution was less formal and not obligatory. Occasionally meat would not undergo a secondary distribution and this appeared to be a factor of size. When the amount of meat was small, little or no sharing occurred at the secondary stage. When there was sufficient meat, all households in the camp received a share. In larger camps and when there was less food the owner of the meat decided who should receive a share but there was no correlation with either kinship or proximity.

During meal sharing, the cook, almost always a woman, distributes plates of stew to other households. These are eaten by the women and children of that household. Additionally, a plate of food is sent to the *mbanjo*, the communal structure located centrally in the camp previously discussed in chapter 2. This share is eaten by the adult men of the camp. Kitanishi (1998) suggests that by sharing meals in this way women give away most of the food they cook. Conversely much of the food a woman and her family eat is provided by other households.

Market integration and the economy of the Mbendjele

History of contact between pygmies and farmers

Genetic data suggest that the Central Africa Pygmies share a common origin. Estimates suggest Pygmies diverged from other African populations at either 54,000 or 90,000 YBP and that Western Central African Pygmies share a relatively recent origin at about 2,800 YBP (Verdu et al. 2009). Despite the deep shared ancestry, Pygmies in this region display a high degree of linguistic heterogeneity. Whilst hints of an ancestral tongue can be found in shared words - particularly those relating to the forest, plants and animals - Pygmy languages belong to the Bantu and Oubangian language families. As such the BaYaka who speak a language belonging to the Bantu C10 tree have more in common, linguistically, with their non-Pygmy neighbours than they do with the Baka who speak a language of the Gbanzili Oubangian group (Bahuchet 2012). This attests to the fact that the Pygmies in this region are far from isolated but have a long history of interaction with non-Pygmies. Ethnographic and archaeological data suggest that trade has been an important part of the interaction between pygmies and their neighbours (Bahuchet & Guillaume 1982), with some going as far to suggest that such a relationship was obligate (Headland 1987, Bailey et al. 1989). Whilst the theory that equatorial forests are unable to support a purely hunter-gatherer lifestyle has come under strong criticism (Bahuchet et al. 1991, Yasuoka 2006 & 2010), the fact remains that market integration is not a recent feature of Mbendjele society.

Changes over the recent decades

That being said, recent decades have seen considerable shift in the lifestyle of many Mbendjele. As discussed in chapter 2, our study populations reside within a logging concession managed by Congolaise Industrielle des Bois (CIB). Camps were situated along

the roadside, a few hours drive from the timber processing facility at Pokola. Exploitation of timber has led to significant changes in the region over the last twenty years. Roads, built to aid the logging, have made previously isolated areas of the forest increasingly accessible. Towns and villages in the region have seen rapid expansion, as local residents are attracted to utilities such as hospitals and schools and as a large population of workers is brought to the area by CIB (Poulsen et al. 2009). Large villages of Pygmies are situated on the outskirts of Pokola, where they live a largely sedentarised life, many making a living from wage labour. However, even for the un-sedentarised Mbendjele, including those on whom this thesis is based, their way of life has been greatly impacted by these changes.

This area of Congo is poorly suited to the rearing of livestock. The protein needs of the population are largely met through wild foods, a combination of river fish and bush meat. This has meant that the amount of bush meat traded in the region increased dramatically over the last decade (Poulsen et al. 2009). Many Mbendjele, including the mobile groups, are active participants in the bush meat trade.

Traders daily travel the roads passing by Mbendjele camps, with some even taking up temporary residence in the camps. Where the Mbendjele have access to markets, usually via traders, who travel the logging routes and sometimes reside temporarily with the Mbendjele, this impacts on the value curve of held resources. Under these conditions meat no longer has diminishing returns, but rather its value increases linearly with the amount acquired (Figure 1.) as traders offer what is, for the Mbendjele, a limitless demand for game. Furthermore, the variance in productivity has also been impacted by development in the region. Access to trade is not unidirectional and Mbendjele are now able to buy a range of cultivated foods, as well as more luxury items such as alcohol and tobacco. Land management policy in the region has meant that some Mbendjele have gained access to

fields of their own and have transitioned to a small scale horticultural system. Access to foods such as manioc and plantain, be it via trade or horticulture, has greatly reduced the stochasticity of the hunter-gatherer diet, allowing families to reliably acquire only as much as they need. The likelihood of both shortfalls and surpluses has been reduced, and importantly, this will tend to decrease short term inter-household variance.

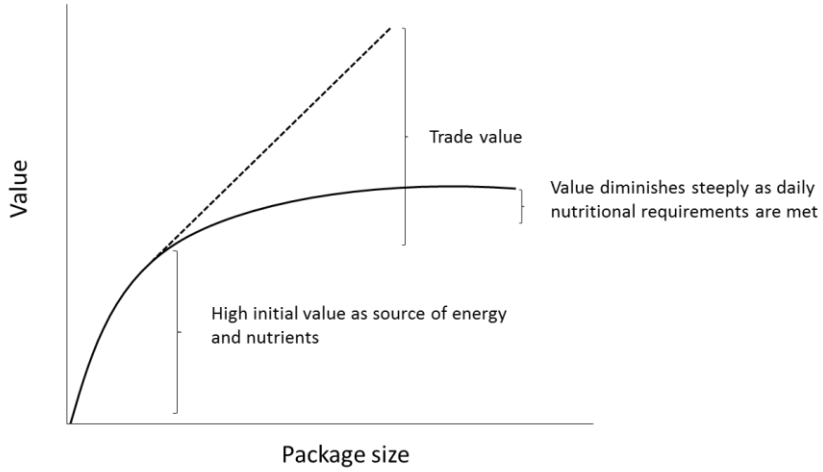

Figure 4.1. Value curves of increasing resource package size in the absence (solid line) and presence of trade (dotted line). Selling surplus food means that increasing amounts of resources will still have increasing value.

Our three study sites present a range of market exposures. The people of Ibamba have access to cultivated foods by means of their own gardens but have little access to trade, living as they do in a region of the forest not undergoing current exploitation and on a road which sees infrequent use. Masia and Longa are situated on a busy trade route, connecting Pokola to a number of villages and towns to the East. As such both camps have access to trade. Of these two, only the people of Longa had any fields or gardens, though on a

smaller scale to Ibamba. In Masia access to cultivated foods was solely via trade. As such these three camps provide an opportunity to examine the impact market integration as a whole has had on food sharing whilst also disentangling the effects of different integration factors. Table 1 provides a summary of the different integration factors in the three camps. A major difference is between the two connected camps (Longa and Masia) and the isolated camp (Ibamba). The product of this is that in the connected camps residents were able to sell both game and non-meat forest products and able to buy cultivated carbohydrates and other trade goods. Additionally, both of these camps had access to snares, shotguns and ammunition. The other large difference was whether camps had access to cultigens via horticulture. This is largely a product of how well established a camp is and thus differentiates Masia from Ibamba and Longa. A third point of comparison is between contemporary and previously published data (Kitanishi 1998). Whereas all three contemporary camps had access to cultigens, either through trade or horticulture, the forest camps studied by Kitanishi were reliant on wild, foraged foods.

Table 4.1. Degree of integration in the three study populations and previously published data.

Study population	Ibamba	Longa	Masia	Kitanishi 1998
Trade	no	yes	yes	no
Access to guns and snares	no	yes	yes	snares only
Practiced horticulture	yes	yes	no	no
Cultigens	grown	grown & bought	bought	none

I predict that both access to cultigens and the ability to sell foraged resources will lead to a decline in food sharing as both factors reduce inter-household variance in value. By providing a reliably accessible source of calories, cultigens reduce short-term

unpredictability. All households can dependably access cassava and plantain as and when it is required and differences between households in resource holdings should be low. Whilst foraged resources such as game are still likely to exhibit high household variance, the ability to sell surplus means that it is no longer subject to rapidly diminishing returns. As such its value to the resource holder is as great as to other households and thus transfer is unlikely to occur.

4.2 Methods

Data on the diet and sharing of the Mbendjele were collected using systematic observation in the three camps (see methods chapter for full details of data collection). Except in Masia, hunting productivity was calculated based on the total number of animals brought into the camp over the entire period of data collection. In Masia the high quantity of animals brought to the camp and the spatial structure of the camp precluded a reliable measure of total number of animals returned during the study period. In this case only those animals brought to the camp by members of households currently undergoing observation were recorded. Since all households were observed equally and evenly across the day and over the entire study period, this allowed us to calculate an estimate of hunting productivity for the camp.

Frequency and duration of foraging trips were reconstructed from scan data (see methods chapter for details on scan data collection). As scans were collected hourly, prolonged absences from the camp are observable in the data set. Besides foraging trips there are numerous reasons why a person may be absent from camp. To try and exclude the most frequent of these, such as collection of fire wood, collection of water, washing and using the toilet we only counted an absence from 3 consecutive scans as a foraging trip. As the

scans collected in Longa were non-sequential, data on foraging trips are not available for this camp.

Caveats and limitations

The use of scan data to reconstruct foraging trip length has several advantages, most notably it is a relatively fast way to collect data on a number of individuals simultaneously, but it has several significant limitations. Firstly, in order to account for absences unrelated to foraging, it excludes any foraging trip of less than three hours. As such the estimates of time spent foraging reported in this chapter are likely underestimates of total foraging trip length. Unfortunately, it is not possible to try and account for this with current data, but from my time spent with the Mbendjele I suggest that the frequency of foraging trips of less than three hours is low, hence why this cut off point was chosen. A notable point is that trips to gardens and fields, where present (Ibamba and Longa), would often be shorter than three hours, as such these are also excluded from the estimates of time spent foraging. In some ways this is advantageous, giving an estimate of foraging effort rather than economic effort, nevertheless, this needs to be borne in mind when interpreting the results.

4.3 Results

Foraging effort and hunting productivity

On average Mbendjele women spend a quarter of daylight hours out of camp engaging in economic activities (e.g. foraging or gardening). Men on average spend just under 40% of daylight hours involved in economic activities outside of camp. Whilst there is little difference between the camps in the proportion of time invested in economic activities, the

duration and frequency of trips vary (table 2). In Ibamba foraging trips were on average longer than in Masia but less frequent.

Table 4.2. Length, frequency and proportion of time spent foraging by adults in Ibamba and Masia.

Sex	Camp	Mean length of trips (hours)		Trips per day		Proportion of daylight hours spent out of camp	
age groups		all ages	<60 years	all ages	<60 years	all ages	<60 years
Male	Ibamba	6.98	7.28	0.64	0.73	0.38	0.47
	Masia	-	4.82	-	1.1	-	0.41
Female	Ibamba	5.60	5.93	0.49	0.54	0.24	0.28
	Masia	-	3.54	-	0.88	-	0.27

A total of 22 animals were brought into the camps during the observation period (table 2). Hunting productivity varied considerably between the three camps. In Masia rate of returns was 0.48 animals per man per day. In Longa the return rate was 0.04 and in Ibamba 0.02.

Table 4.3. Game brought into three Mbendjele camps, with the number of times they were underwent distribution.

Masia. Camp size: households - 9, Men -8.

Systematic observation: Returns over 3 days.

Mbendjele name	Common name	Scientific name	Number brought into camp	Number of primary distributions	Number of secondary distributions
Masome	Peter's duiker	*Cephalophus callipygus*	5	0	0
Sengay	Unknown duiker	*Cephalophus sp*	3	0	0
Mboko	Blue Duiker	*Philantomba monticola*	2	1	0
Ikadi	Pangolin	*Manis tricuspis*	2	0	0
Kudu	Forest hinged back tortoise	*Kinixys erosa*	1	0	0

Longa. Camp size: households -10, Men-7. Observation period 4/04/2014 – 22/04/2014

Ad lib sampling over 24 days.

Mbendjele name	Common name	Scientific name	Number brought into camp	Number of primary distributions	Number of secondary distributions
Masome	Peter's duiker	*Cephalophus dorsalis*	3	0	0
Sengay	Unknown duiker	*Cephalophus sp*	1	0	0
Ikadi	Pangolin	*Manis tricuspis*	1	0	0
Kudu	Forest hinged back tortoise	*Kinixys erosa*	1	0	0

Ibamba. Camp size: households -14, Men-10

Ad lib sampling over 19 days.

Mbendjele name	Common name	Scientific name	Number brought into camp	Number of primary distributions	Number of secondary distributions
Mokwake	Dwarf crocodile	*Osteolaemus tetraspis*	2	0	2
Ngomba	Brush tailed porcupine	*Atherus africanus*	1	0	1

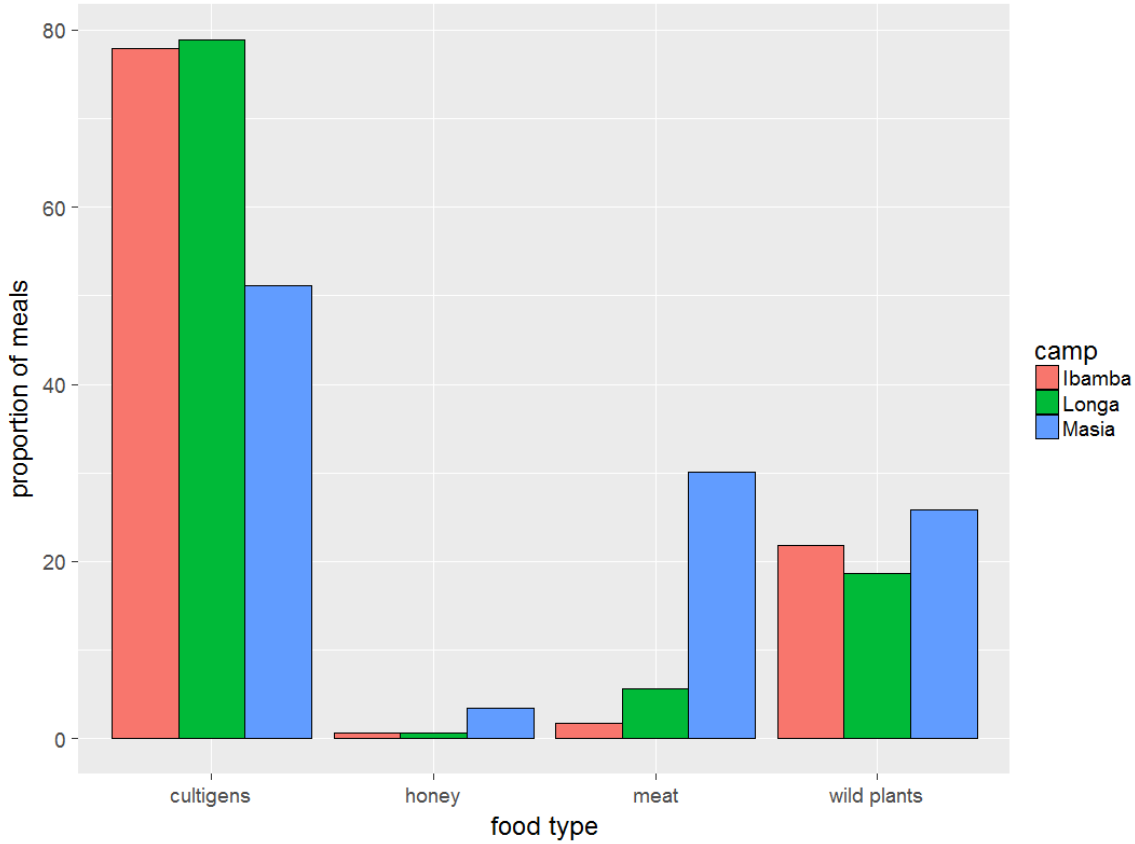

Figure 4.2. Percentage of all meals in three Mbendjele camps which contained cultigens, honey, meat or wild plants

Diet

A total of 589 meals were observed across the three camps. Here we define meals as any event in which food is consumed. As such just under a third of these "meals" involved a single person (n=182) or were relatively small snacks, such as fruits and nuts shared by a group of people. Typically, a larger meal would be prepared once or twice a day, in the evening and sometimes also around midday. Portions of the evening meal would often be set aside for the following morning. These meals often consisted of a stew of meat, palm oil and wild plants, where available. This would be accompanied by a starch such as manioc, wild yams, plantain or rice. When and where meat was not available the stew would often be replaced with *djabuka*. *Djabuka* is a dish of mashed cassava leaves, widely consumed across Congo and the rest of Central Africa and known in Lingala as *saka-saka*. As with the stew, this is accompanied by a starch, often the roots of the same cassava plants. Across all camps cultigens are an integral part of the diet (figure 2). This is particularly the case in Ibamba and Longa where cultigens were present in 78% and 79% of meals respectively. In Masia the greater hunting productivity translated to greater amount of animal protein in the diet. In this camp just under a third (30%) of meals contained meat and just over half (51%) cultigens.

Food sharing

Primary distribution

There was only a single incident of primary distribution observed (table 3). Two men, who had gone on a hunting trip with a single shotgun, returned to camp with a blue duiker, the smallest species of antelope that the Mbendjele commonly hunt. The duiker was divided lengthways into two equal pieces, each man taking a half. This contrasts with the highly formalised primary

distribution previously discussed. This may suggest that, despite the fact that only one of the men could make the killing shot, they did not distinguish between themselves in regards to either the role or amount of investment in the acquisition. In this case, gun ownership also did not appear to confer any greater claim to the animal or specific parts thereof.

Secondary distribution

Overall secondary distributions were rare, with only three recorded events for the 22 animals returned (table 2). However, all 3 events occurred in a single camp (Ibamba) and accounted for 100% of the game brought into that camp. During these distributions, each household in the camp received a portion of the meat. The majority of the meat was retained by the acquirer's household. Whilst I do not have quantitative data on the amount each household received, there was evidence of unequal distribution. In one of the cases a dwarf crocodile was caught with each household receiving enough meat for a single meal. Both the acquirer's household and their closest neighbour retained or received enough meat for several meals over the following days, suggesting that secondary distributions may exhibit uneven distribution patterns, though it is unclear whether proximity or some other factor of the relationship between these two households led to this bias.

Secondary distributions were entirely absent from both Masia and Longa. In these camps a large proportion of the meat was sold. Small animals such as blue duiker, pangolins and reptiles were either sold whole or retained completely by the hunter's household. Larger animals, such as Peter's duiker, were butchered in the camp. Usually the internal organs and head would be retained by the hunter and the rest of the animal sold to traders. Organs such as the liver would be roasted soon after being removed and shared with many of those

present. In this case the distinction between a secondary distribution and meal sharing becomes blurry. The cooking is usually focused within the hunter's household but often other people, particularly children, participate. For this analysis I have classified such behaviour as meal sharing even when someone outside of the hunter's household is involved in the cooking. Similarly, other food stuffs which are consumed with little or no processing have been included in meal sharing. This includes foods such as fruits and nuts. I feel justified in classifying this as meal sharing as the food is eaten soon after being shared, with both the donor and recipient participating in the meal.

Honey sharing presents a unique example which deserves specific mention. In many ways honey is shared similarly to organs and fruit. Honey is distributed to and consumed by all present in the immediate area at the point the acquirer returns to the camp. However, unlike both organs and fruit, households will often retain some amount of their honey. In this way it also resembles the secondary distribution of meat. I have not included honey sharing in our analysis of secondary distributions or meal sharing as it seems to have its own unique pattern. Honey was brought into camps infrequently during the study period. Thus we do not have sufficient data to provide an in depth analysis. However, observations of honey sharing in camps, as well as the observed practice of entire households accompanying men out on honey collection trips, suggest that honey sharing deserves specific attention in future work.

Meal sharing

Over the 7 camp days a total of 589 meals were observed. Of these, 47% were shared beyond the cook's household (table 3). Shares of meals were rarely directly solicited. Meal sharing most commonly involved the cook, usually an adult woman, dividing the meal into several

portions. The cook would then send these plates to other households, often engaging the help of children to do so. Members of the recipient household would eat together from the same plate. Occasionally shares of food would be sent to a group of adult men who would then eat as a group. This is similar to a previous description of meal sharing where the men would eat separately from their families (Kitanishi 1998). However, during our data collection such behaviour was relatively rare; more often men would dine with their families.

Excluding meals which were not shared at all, on average 60% of the food went to people outside of the household (n=277, SD = 0.35), to 1.59 other households on average (SD = 1.0). Differences in sharing breadth and depth between camps were small (Table 3). There was no significant difference in the depth (proportion of the food given away) of sharing between the three camps (Kruskal Wallis H=5.98, p = 0.05), but there were significant differences in breadth (number of recipients) (H= 8.53, p = 0.01).

Table 4.3. Descriptive statistics of meal sharing at the three study sites. Sharing breadth refers to the total proportion of a meal given away. Sharing depth refers to the number of individuals who received a share who were not members of the producer's household.

Camp	Number of meals	Meals shared	Sharing depth Mean (SD)	Sharing breadth Mean (SD)
Masia	234	113 (48%)	0.58 (0.25)	1.77 (1.15)
Longa	142	63 (44%)	0.63(0.27)	1.34(0.74)
Ibamba	213	101 (47%)	0.58(0.25)	1.6(0.98)
Total	589	277 (47%)	0.60(0.26)	1.59(1.00)

4.4 Discussion

There is a considerable body of literature on the effects of sedentarisation on hunter-gatherers. Often this involves either a comparison of hunter-gatherers living in towns and settlements with historic data (Hawkes et al. 1987, Gurven et al. 2002) or looks at differences between settled and mobile hunter-gatherers (Salali & Migliano 2015, Page et al. 2016, Smith et al. 2016). A common limitation with such work is that the process of sedentarisation entails multiple and varied changes to the environment. Market integration, access to sanitation, health care and education, changes to diet and greater stability of social networks are all possible consequences of sedentarisation and may impact hunter-gatherer behaviour (Salali & Migliano 2015, Smith et al 2016), health and fertility (Page et al. 2016). Furthermore, the results in this chapter highlight another weakness of the comparison of settled and mobile hunter-gatherers. Even those groups who maintain their mobility are greatly impacted by some forces such as market integration. Though they retain their mobility and, to some degree autonomy, the participants in this study choose to live by roads. In doing so they gain access to trade, a greater flow of information and easier access to the forest. A graphical representation of foraging routes by the Mbendjele living in Ibamba (Fig. 2) shows how they frequently make use of both the maintained roads and also long abandoned logging tracks to improve foraging efficiency. The Mbendjele choose to live this way despite the costs. Threat and harassment by ecoguards, police and other non-Pygmies are everyday occurrences for the Mbendjele. At times this becomes too much, triggering a move away from the roads and into the forest. But the fact that such moves are often temporary speaks to the value the Mbendjele place in being connected to the wider world.

The results presented here highlight two of the benefits the Mbendjele gain from integration: access to cultigens and access to hunting tools. Amongst this study population these appear almost obligatory. In the absence of shotguns and access to wire for snares, hunting productivity is greatly reduced. In all three camps, cultigens, particularly cassava and plantain, form the core of the diet. Given this, is it fair to describe these contemporary Mbendjele as inhabiting a foraging niche similar to the hypothetical "social foraging niche" I described in chapter 1?

Despite the importance of cultigens in the Mbendjele diet, the principal economic activity of the Mbendjele remains foraging. Whilst the data on foraging trips does not precisely discriminate between foraging and gardening, as both appear as an absence during the scans, from our experience most trips to gardens and fields were of a shorter duration than 3 hours. Any such trips are not included in our estimates of time spent on economic activities. Averaged, men spend between 4 and 5 of the 12 hours of daylight out of the camp foraging. For women, the average is smaller but not insignificant at around 3-4 hours. It is clear that these people are primarily foragers. That being said, how and what they forage has been greatly impacted by market integration. Hunting with guns and snares are now the favoured methods of hunting. Tools such as crossbows, spears and nets are no longer readily available. But it is not only men's foraging that has been affected. In those camps with access to trade, both women and men actively forage for non-meat forest products which they can sell. Chief amongst these are *koko* leaves (*Gnetum sp.*), a wild growing vine used frequently in Congolese cooking, and *ngongo* leaves, a plant which dominates large parts of the forest understorey, which are used in the packaging of processed cassava. These plants are sold for relatively little, a household would typically make between 600 – 1000 central African francs from a foraging

trip. This is enough to buy cassava for an averaged sized family for 2-3 meals. A key trait of immediate return foragers is that the payoff occurs at the point of labour or soon after (Woodburn 1982). Despite the prevalence of cultigens and the importance of trade, this still describes the economic practices of the Mbendjele. The adoption of cultivation by the Baka in Cameroon appears to show a similar reluctance to move away from immediate return practices (Kitanishi 2003). The Baka's favoured crop is plantain. This requires relatively little long term investment. Plantain is also an important crop for the Mbendjele. That the Mbendjele in this study still retain a fundamentally immediate returns outlook is evidenced by their low probability of future discounting in comparison to Mbendjele residing in the town of Pokola (Salali & Migliano 2015). Given the above it seems reasonable to describe these contemporary groups of mobile Mbendjele as immediate return foragers. Are they therefore suitable models for examining the social foraging niche and its role in human evolution? Clearly this cannot be assumed. In the following section I discuss the impact of market integration and associated factors on food sharing which show the complex interaction between market integration and behaviour.

Food sharing amongst contemporary Mbendjele has both declined and remained constant

An important finding is that different forms of sharing have been differently impacted by market integration and associated factors. Whilst a decline in sharing is observed, it is not correct to simply say that this is associated with the increase in predictability that results from market integration as different types of sharing are impacted by different factors. Meal sharing appears resilient to market integration related changes, whilst both primary and secondary distributions of meat have declined.

In this study meat sharing, at either the primary or secondary distribution stage, was rarely observed. Meat has a high nutritional value, not only in terms of its calorific content but also as a source of proteins, fats and a range of micro nutrients. Furthermore, it comes in large indivisible packages, with a high variance in encounter and acquisition rates. This explains why meat is shared to a greater extent in a number of foraging societies (Kaplan et al. 184, Kitanishi 1998). We might therefore predict that meat sharing is the most likely area to be impacted by declines in variance. However, our results suggest this is an oversimplification. Whilst decline in the secondary distribution may be a result of such factors, it appears more likely that a decline in primary sharing results from changes in the hunting practices of the Mbendjele, specifically, a decline in large scale cooperative hunting.

A highly formal primary distribution of meat was absent from our study. Whilst a single incidence of an animal undergoing a primary distribution was observed, this was not according to set rules, rather, each man took an equal share of the meat. This decline of sharing does not appear to result from changes in variance resulting from market integration but the result of changes in hunting practices. Throughout the study period we observed three main forms of hunting, hunting with shotguns, trapping with snares and capture of animals using hands or simple tools such as sticks. The latter of these includes the incidental hunting of slow moving and easy to acquire animals such as pangolins and tortoises, where encounters were not pursued specifically but were a by-product of movement through the forest. However, also included in this category was crocodile hunting. Men specifically set out to hunt crocodiles, travelling to certain areas of the forest where they are likely to be. Each of these hunting practices usually occurs in small groups, pairs or alone. In contrast spear and net hunting are undertaken by large groups of people. Mean group size for spear hunting has been calculated

as six, whilst for net hunting groups on average include 25 individuals (Kitanishi 1996). Furthermore, rules of primary distribution relating to spear and net hunting not only included those actively participating in the activity but also those who provided the tools of acquisition. For example the owner (*konja*) of the animal, who is responsible for the division and distribution of the meat, is not the person who made the kill but the owner of the tool used to incapacitate the animal, be it the spear that made the first blow or the net which caught an antelope (Kitanishi 1998). In his description of sharing by the Aka of central Africa, Bahuchet (1990) details how participants in the acquisition and killing of an animal, owners of the tools of acquisition and those involved in the transport and butchery of the animal all received specific parts of the animal. Given the formality of these rules, it seems likely that, had net and spear hunting occurred during our study, we would have also observed primary sharing as previously described (Kitanishi 1998).

Large scale cooperative hunting was absent from our study though informants claimed they still had nets in the villages. However, cooperation was still integral to the hunting of the Mbendjele. Men from the same household, typically close kin such as a father and son, often cooperated in snare hunting, taking it in turns to walk the trap line. However, men cooperating in hunting with firearms often formed partnerships beyond the household or kin ties. Whilst father-son and fraternal hunting partnerships were not infrequent, the same was true of unrelated hunting partnerships. Indeed, such partnerships are necessary given that a third of men in our study lived in camps with no male kin of a suitable age to accompany them hunting. Whilst such cooperation did not result in a formal distribution of meat as previously described, nevertheless a distribution of resources still occurred. However, the distribution either

involved each man taking an equivalent number of animals, or else the equal sharing of money once the animals were sold.

The lack of primary sharing reflects changes in the foraging strategy of Mbendjele hunters rather than an increase in the predictability of the diet. During the primary distribution, meat is given to all those involved in the capture of the game (Kitanishi 1998, Lewis 2008 & 2015). Increased access to tools such as shotguns, electric torches and wire snares has greatly increased the efficiency of solo or small group hunting. Other hunting methods, most noticeably spear and net hunting, with mean group sizes of six and twenty five respectively (Kitanishi 1996) are rarely practised. Thus, the decline in primary distribution reflects the reduced amount of cooperative hunting. Primary distribution does still occur in those cases where men cooperate in hunting and noticeably after honey collection.

When hunters have access to markets, as is the case Masia and Longa, they sell a large proportion of all the meat they acquire. Often a small amount of meat is retained by the producer's household. Either a small animal such as a pangolin or tortoise is kept, or in the case of big game the head and internal organs are retained. These portions were not distributed around the camp but were cooked by the women of the hunter's household. The initial calories of a food package are of large value to the producer household (Blurton Jones 1984) and the retention of this portion without subsequent division is as we would expect. It is those excess calories which would have little additional benefits to fitness which are sold to Bantu traders and which in the absence of trade would have been shared with other camp members.

Meal sharing was the only distribution which, contrary to our prediction, does not appear to have undergone decline. It was prevalent in each of the camps and, to some extent, practised

by every household. Thus, hunting productivity, trade and horticulture appear to have little effect on either the frequency of meal sharing or its form. This suggests that its occurrence is not directly a response to variance in value. Cultivated foods were an important constituent of the diet in all three camps, suggesting that both trade and horticulture provide reliable access to resources such as manioc, plantain and rice. These resources are less prone to shortfalls than wild foods.

A greater efficiency in time to calories acquired reduces the impact of environmental variation. For example, the Mbendjele are able to quickly access fields in the periods between rain showers which would not provide enough time for an effective foraging trip. Furthermore, large investments in the form of travel time and search effort mean that even small package wild foods such as nuts and yams should be harvested in large quantities. In contrast, it makes sense to acquire the amount of cultivated foods not subject to steeply diminishing returns, either when harvesting or buying such resources. Thus, cultivated foods are less prone to both shortfalls and surpluses and lead to relatively low variance between households.

Our data collection methods, which focus on only a section of each camp at any given time, preclude the calculation of household resource holding synchronicity. However, it was not uncommon to observe a woman sending a plate of manioc and *djabuka* to the household of another woman who, at that very moment, was preparing just such a meal.

Other studies of food sharing under relatively stable conditions have also observed meal sharing. The diet of Ache living on reservations in Paraguay constituted 80% cultigens (Gurven et al. 2001). Despite this, meal sharing was common. The authors of this paper suggest that this may be the result of economies of scale. By which they mean that, if production is subject

to large fixed costs, such as a long travel time to reach the harvest site, then the additional costs of increased harvest size may be relatively small. Under such conditions a reciprocal system whereby partners take turns in paying the large fixed cost whilst providing a benefit to both parties could evolve. In the case of the Ache, the fields where manioc and other cultigens grew were located a considerable distance from the place of residence. Thus, it is reasonable to suggest that food sharing was occurring because people took turns visiting the fields, and thus held resources, on any given day.

In the case of the Mbendjele such an explanation does not work. Firstly, for those accessing cultigens via trade an economy of scale is not present. Additionally, even for those Mbendjele practising horticulture the situation differs markedly from that reported for the settled Ache. Fields and gardens were situated relatively close to the camp site and there were no other sources of large fixed costs in harvesting cultigens.

The Mikea of Madagascar present an interesting case study in the food sharing literature, as a group who adopted a forager lifestyle relatively recently, sharing, as they do, a shared history with Malagasy agriculturalists, pastoralists and fishermen (Stiles 1991, Tucker 2004). Interestingly, the Mikea share relatively little, in comparison to other forager people. Meat and honey are rarely shared beyond the household, but “porridge”, by which the author means cooked wild and cultivated plant foods, is shared often (Tucker 2004). In this way, the sharing of the Mikea superficially resembles that of the Mbendjele. Raw food is shared infrequently, whilst cooked foods are distributed often. In this case, again the author invokes economies of scale, suggesting that the large fixed costs processing and cooking involved in preparing porridge could lead to reciprocal sharing.

A shortfall of this argument is that this turn taking would take place over a matter of hours rather than days. Daily synchronicity of porridge, in this case the chance that more than one household will have the same porridge on a given day, was very high (Tucker 2004). It did not appear that sharing porridge allowed households to avoid fixed costs of food preparation, but perhaps covered the short-term shortfalls that arise as a result of intensive food preparation.

In the light of our failure to find an economy of scale explanation, it is worth considering other explanations for why meal sharing persists even under stable conditions, or how we might gain insight into this. One potential explanation is that whilst trade and cultigens reduce short term daily variance they may not impact upon longer term and less frequent sources of variance such as illness and injury. There is evidence that amongst the Ache those who share more than the average received a greater amount of food when sick or injured (Gurven et al. 2000). Sharing even under stable conditions could theoretically serve as a signal to others and thus explain why sharing persists even with access to cultigens. Of course, if cultigens provide a source of food even for those households with sick or injured persons, then we would still expect this form of sharing to decline. The impact of illness and injury on hunter-gatherer production is not well understood, let alone the extent that cultigens have been able to buffer this. Future work would do well to examine the interactions between health, production and sharing.

In addition to what it can tell us about the proximate and ultimate explanations of Mbendjele food sharing, the results are also of significance to those interested in the development and management of Northern Congo, its resources and the wellbeing and rights of the Mbendjele. We have examined the effect of external pressures on the Mbendjele emerging from two

sources: a) the increased demand for bush meat and other forest products that comes from a larger and more easily accessible market; and b) the land use and hunting policy brought in by the Congolese government. It is critically important that we understand how both development and policy impact upon the lives of indigenous peoples. By highlighting sharing we have revealed how complex the interactions between these external forces and hunter-gatherers can be. On the one hand the resilience of meal sharing, despite the changes to the environment of the Mbendjele, can be seen as reassuring, though by the same logic the decline in meat sharing and the practice of communal dining by men could be seen as a warning sign of the loss of hunter-gatherer culture. In truth, the Mbendjele are neither resilient nor fragile, but plastic.

Perhaps the most important result, in terms of policy and protection is the absence of "traditional" hunting methods, which led to the decline in primary sharing. The primary means of hunting by Mbendjele in this study, hunting with shotguns and snares, are forbidden across much of their home range. The prevalence of these hunting methods, despite this legislation, is of considerable significance. Firstly, it suggests that either the policy and/or its policing is ineffective. The Mbendjele choose to use these methods, presumably because of their greater efficiency, despite the significant risks and costs involved in engaging in illegal activity. Furthermore, the characterisation of the Mbendjele as spear and net hunters is in reality false. Whilst such methods are within living memory this will likely change rapidly. Even at present when those who know how to undertake such types of hunting are present within a camps, a lack of equipment and perhaps social infrastructure precludes such activities. My hunting data from Ibamba show this clearly. Without access to shotguns or snares, hunting productivity is

extremely low. Clearly there are significant barriers to adopting the “traditional” hunting methods favoured by the government and conservationists.

Conclusion

Hunter-gatherers are not living fossils, as with all societies they are under constant flux. This poses both a problem and an opportunity for evolutionary researchers who look to hunter-gatherers as a window onto our evolutionary past. We need to be wary of oversimplification. Market integration is not a single process but rather a suite of correlated forces. Similarly, I have shown that categorizing all food sharing as a single behaviour, even within a society, masks its actual complexity. Mbendjele sharing has at least two distinct functions, the facilitation of cooperative hunting and the reduction of variance. The fact that the secondary distribution has declined whilst meal sharing persists, despite a probable shared function, suggests that the often-overlooked proximate mechanisms of sharing have a profound effect. In the following chapter, we take a closer look at meal sharing. By examining the relationships of those who share food with one another we hope to provide fresh insight into both ultimate and proximate explanations for this behaviour and better answer why this form of sharing appears so resilient.

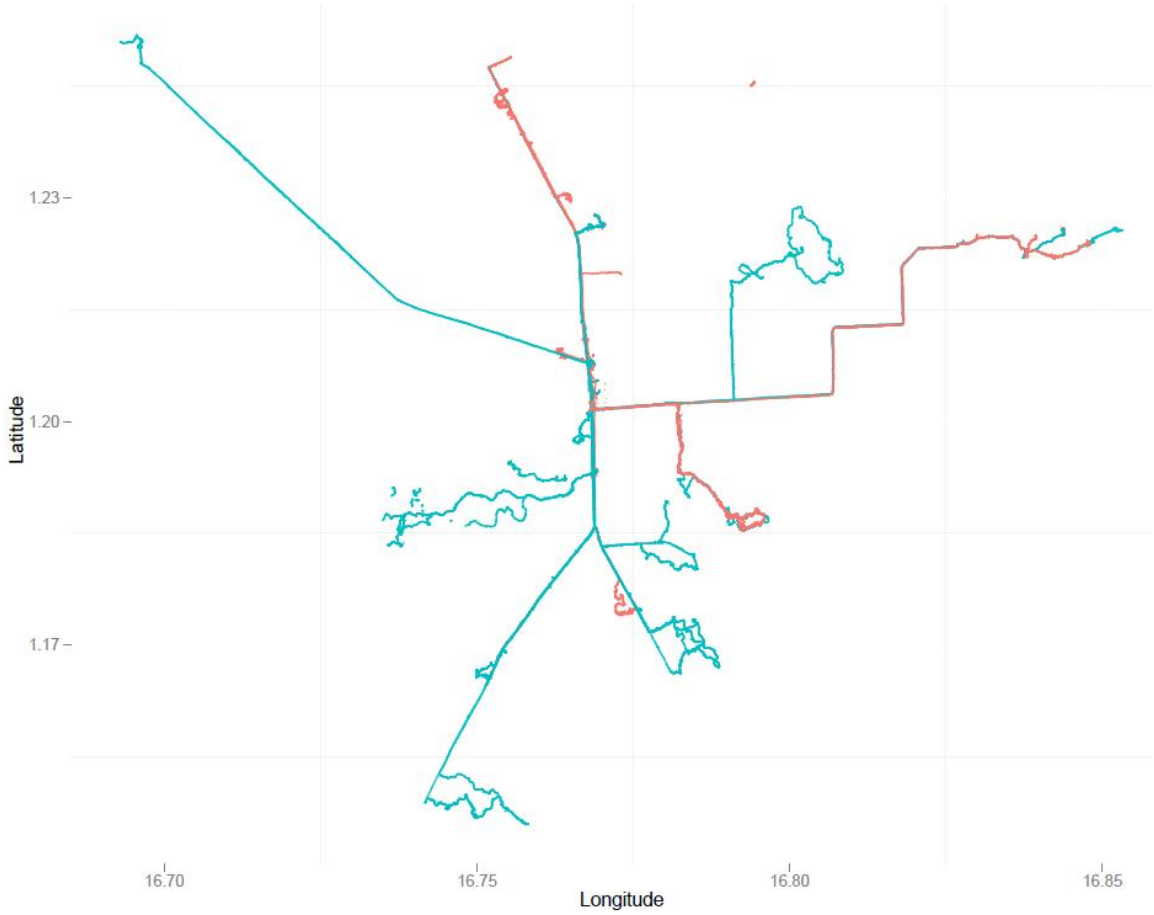

Figure 4.2. Map of foraging routes undertaken by male (blue) and female (red) Mbendjele from Ibamba.

5. The function of meal sharing: reciprocal altruism and kin selection

In the previous chapter I showed that meal sharing was the most resilient form of food sharing, in regards to changes in diet and foraging practice. In the present chapter I address the question of the function of meal sharing. Kin selection and reciprocal altruism are the best supported explanations for sharing in forager societies. Here I examine meal sharing at the dyadic level to measure the extent which households share with kin and to gauge the levels of reciprocity. In doing so I address whether kin selection or reciprocal altruism best explains sharing in this population and discuss the role kinship may play in stabilising cooperation. I extend the analysis in the previous chapter, comparing meal sharing in the three contemporary camps, as well as with previously published Mbendjele sharing data. Across all groups meal sharing occurred mainly at the dyadic level, which is to say sharing was not generalised but targeted at specific sharing partners. Furthermore, all groups show positive dyadic reciprocity. The importance of kin provisioning varies by camp, partially as a result of variation in group structure, but possibly also as the result of access to reliable foods. The results reported here suggest that meal sharing may serve multiple functions, reducing risk by means of reciprocal sharing, and provisioning of kin. The relative importance of these two roles is not static but a product of the ecology and social structure of the camps.

5.1 Introduction

Until the recent resurgence in support for group selection (Gintis et al. 2003, Henrich 2004, Nowak et al. 2010), discussion on the evolution of cooperation has focussed on two mechanisms, kin selection and reciprocal altruism. Hamilton (1964) provided the most well-known formulation of kin selection. A genetically inherited cooperative trait will spread in a population when the costs to the co-operator are less than the benefits to the recipient

multiplied by the probability that they share that gene (rB > C). Kin selection has most famously been used to explain eusociality in insects (Hamilton 1964), but has been applied to cooperation by a wide range of animals (Clutton-Brock 2009).

In contrast, examples of reciprocal altruism in non-human animals have proven difficult to find (Clutton-Brock 2009). Food sharing by vampire bats provides a notable example (Wilkinson 1984). In his seminal paper, Trivers (1971) describes how cooperation can spread through a population if the net-benefits of cooperative acts are greater for altruists than for non-altruists. This can occur when cooperation is preferentially directed at altruists. Several mechanisms by which this may occur have been proposed. Direct reciprocity occurs when altruists decide who to cooperate with based on previous interactions (Axelrod & Hamilton 1981). Simply put, A helps B when B has previously helped A. In contrast, indirect reciprocity does not require the repeated interaction of specific dyads. Instead, altruistic acts should be directed at those who have exhibited cooperative behaviour, irrespective of past interactions. In other words, A helps B when B has previously helped C , D or any other group member. Such a system is clearly dependent on altruists possessing reliable information on the previous interactions of other group members (Nowak & Sigmund 1998, 2005). Finally, generalised reciprocity supposes that altruists should choose to help others based only on their previous experience, independent of any quality of the potential recipient (Pfeiffer et al. 2005, Rutte & Taborsky 2007). In other words, cooperate in a cooperative environment, defect in a selfish environment.

Understanding the mechanisms by which reciprocal altruism can evolve and be maintained is of significant interest, given its scarcity in non-human animals. Mobility (Lewis et al. 2014), punishment (Fehr & Gachter 2002) and reputation (Nowak & Sigmund 1998, 2005)

have all been suggested as important prerequisites of reciprocal altruism receiving theoretical and experimental support. However, finding evidence of such mechanisms in naturally occurring cooperation has proven more difficult.

Much of the work on food sharing has focussed on whether kin selection or reciprocal altruism better explains the behaviour, with the former receiving greater support (Kaplan & Hill 1985, Allen-Arave et al. 2008). Recently the either-or debate has changed. Analyses now look to highlight the interaction between kinship and reciprocal altruism (Allen-Arave et al. 2008, Nolin 2010, Koster & Leckie 2014, Hooper et al. 2015, Dyble et al. 2016). Two patterns have been observed or suggested. Firstly, that food sharing is the product of independent kin provisioning and reciprocal sharing practices. Food sharing amongst the Mbendjele and the Agta show a distinctive multilevel structure, suggestive of multiple functions of food sharing (Dyble et al. 2016). For the Tsimane there is evidence for both reciprocal sharing (Jaeggi & Gurven 2013) and kin selected provisioning (Hooper et al. 2015).

A second noted interaction between kinship and sharing has been found in a range of forager societies, including the Ache (Allen-Arave et al. 2008), Lamalera (Nolin 2010) Mayanga and Miskito (Koster & Leckie 2014). In these societies people most often share food with kin, but do so in a highly reciprocal manner. The significance of kin biased reciprocity, as I will refer to this phenomenon, has been potentially overlooked, particularly in regards to the evolution of reciprocal altruism. The fact that reciprocal altruism allows for cooperation between unrelated people has led to the suggestion that interaction between non-kin was a key factor in its evolution (Hill et al. 2011). The occurrence of kin biased reciprocity is an important reminder that non-kin are not a precondition for

reciprocal altruism and in fact the conditions under which it arises are more likely between family.

There are numerous theoretical explanations for why reciprocal altruism may be more common amongst relatives. These can be divided into those directly involving inclusive fitness and those that are not affected by kin selection. An example of a mechanism belonging to the latter category would be that kin are more likely to live together over extended periods and as such are more reliable sharing partners. There is simply a higher probability that kin will be around to reciprocate.

A similar mechanism, though not restricted to kin, has been used to explain different levels of reciprocity amongst the Agta (Smith et al. 2016). In camps with high stability, which is to say low rates of migration in and out of the group, levels of reciprocity are higher than in unstable camps. If we think of reciprocal altruism as a simplified inequality; $pB > C$ Where p is the probability of reciprocation, then we are suggesting kin have a higher value of p.

The other reason why kin may be favoured as sharing partners is that the cost to benefit ratio is altered by inclusive fitness. Sharing food with kin has a reduced value of C, as even when they do not reciprocate there are still small inclusive fitness gains which offset some of the costs. Thus we would predict that reciprocity between kin should appear under a greater range of circumstance (higher costs, lower benefits and reduced chance of being paid back).

Whilst these inclusive fitness gains may be relatively small, they could potentially serve to stabilise reciprocity. Because sharing between kin can occur under less favourable cost benefit ratios, this may also have the effect of increasing p. Imagine a situation in which a resource holder must decide how to distribute food between several partners with whom they have shared food in the past. Supposing all factors other than relatedness are equal.

The donor is predicted to choose their kin for the small inclusive fitness gains. In turn, this means their kin should reciprocate more than the other dyads beyond the inclusive fitness effect. With repeated interactions preference for kin should increase further even if the inclusive fitness benefit is small.

This chapter aims to test whether kin selection or reciprocal altruism best explains meal sharing by the Mbendjele. Furthermore, we examine whether kin are preferentially chosen as sharing partners.

5.2 Methods

Data on meal sharing were transformed into values of food transferred between each household-household pair. Such dyadic data are inherently non-independent as each household appears multiple times in the data set. There are several ways to deal with pseudoreplication, including quadratic assignment procedures, as used in the following chapter. For this analysis we use a multilevel formulation of the social relations model (SRM (Snijders & Kenny 1999, Koster & Leckie 2014, Koster et al. 2015)). SRM allow the partitioning of dyadic data into separate giver, receiver and relationship variance components. In food sharing terms, this allows us to take the food shared by dyad *ij* and estimate to what extent it is a product of the generosity or stinginess of household *i*, the neediness of household *j* and the specific relationship between the two households.

This has two benefits. Firstly, the variance partition components (VPC) provide useful information relating to mechanisms of food sharing, particularly in regards to reciprocal altruism. If food sharing is a form of generalised or indirect reciprocity, we would expect to see large giver and receiver VPCs and a relatively small dyadic component. In contrast, direct reciprocity should produce a large dyadic component as specific household pair preferentially engage in sharing.

A second benefit is that, by calculating the correlation between dyadic variance components, we can estimate dyadic reciprocity, accounting for any individual level effects (Kenny 1994).

Previous studies on reciprocity and food sharing have used the dyadic measure of sharing as a predictor when attempting to measure dyadic reciprocity, i.e. X_{ji} is used as a predictor of X_{ij} . Such a method introduces an endogeneity bias (the two variables are correlated) which the SRM avoids (Koster & Leckie 2014, Koster et al. 2015).

I adopt a multilevel formulation of the social relations model suitable for a small dataset with a large number of zeroes (i.e. many dyads were never observed to share food) (Koster & Leckie 2014, Koster et al. 2015). Households are nested within sharing relationships, which denote the direction of transfer. These in turn are nested within dyads. Analyses were performed in R and MLWIN and made use of the R2MLwin package. I firstly present results from an intercept only model and then from models including relatedness and proximity as fixed effects. Relatedness is calculated as the maximum coefficient of relatedness between any two members of the two households. Thus a household in which both the husband and wife have siblings in the camp will have a coefficient of 0.5 with any house in which a sibling is present. A coefficient of relatedness of less than 0.125 was treated as 0. Proximity was calculated as the distance in metres between the entrance ways of the two households. This was measured using GPS data. In Masia the small size of the camp precluded such data. Most households were within 2-3 metres of each other. In this camp a proximity clustering variable was used instead. The camp was clearly split into two clusters approximately 50 metres apart. In the analysis we used a binary variable with dyads classified as within or between clusters.

Along with analysis of meal sharing in Ibamba, Masia and Longa, we also test meal sharing data published by Kitanishi (1998) in the same manner. Kitanishi reports dyadic counts of meal sharing over a number of periods. In this analysis I work with the two largest data sets which relate to a single camp (henceforth M group) over periods 5 & 6 in the original paper. Dyadic relatedness between households was calculated in the same manner as previously discussed for my own data, using genealogies detailed in Kitanishi (1998). Proximity data were not reported in this study, so fixed effect models for this data include only the kinship variable.

Caveats and limitations

The measure of sharing used is based upon a fairly simplistic estimation, assuming for instance, that all maniocs provide roughly the same amount of calories and that all plates of food are roughly the same weight. This relatively crude method was necessary in order to collect a systematic sampling of all dyads but limits the accuracy of the sharing measures. If the aim of this research were to calculate a calorific value of exactly how much food was shared then this methodology would not be appropriate. However, this chapter is concerned with the relationships between people who share food and the relative differences between dyads. It is likely that the methods of estimation have produced noise and thus led to a loss of signal, but I think it less likely that it has introduced any systematic bias that could lead to a false positive result. Of greater importance is the fact that all foods are simply transformed into a calorific value. This is in order to create a measure of sharing that can be easily analysed. However, this measure ignores any non-energetic value that foods may hold. For example, the protein and fat content of meat may hold a value beyond its calorific value. This could lead to it to it being shared in a way that differs from other foods. It is not unreasonable to suggest, for instance, that in terms of absolute

calories a household may share food with related and unrelated people to the same extent but that they offer better quality foods to kin. Any such effects have not been examined in this thesis, but future work in this area can and should address this area.

An important caveat regarding the use of data from Kitanishi (1998), is that the genealogies used to calculate relatedness do not include children. Consequently, values of household-household relatedness are likely to be underestimated relative to the household relatedness of Longa, Ibamba and Masia.

Table 1. Details of sample size and data collection methods. Sample methods: Systematic observation (SO), as detailed in chapter 3, all sharing observed during periods of focal observation were recorded. *Ad. Libitum* (Ad. Lib) All meal sharing events observed during study period were recorded, full methods can be found in Kitanishi 1998.

Sample	Ibamba	Longa	Masia	M group period 5	M group period 6
households	13	11	8	17	17
meals	239	104	256	69	114
meals/household (mean)	18.38	11.56	28.44	4.06	6.71
Standard deviation	10.06	8.90	14.05	2.90	3.29
sample method	SO	SO	SO	Ad. Lib.	Ad. Lib.
observation period	36 hrs	24 hrs	36 hrs	9 days	15 days

5.3 Results

The present project's data

Intercept only Model

Variance partition components (VPCs) can be calculated by dividing the estimated variance for each random effect level (giver, receiver and relationship) by the total of all three, providing an indication of the relative importance of each level. In each camp the relationship VPC was the largest component (Figure 1.). 95%, 78% and 98% of variance in meal sharing was a function of specific household-household relationships in Ibamba, Longa and Masia respectively. Thus overall there were relatively small differences in how much households give and receive but considerable variation how much sharing occurred within specific dyads. In both Ibamba and Masia, giver and receiver VPCs are extremely small (Ibamba - giver = 1%, receiver = 4%; Masia giver = 1%, receiver = 1%). In Longa, however, 22% of variance in food sharing was the result of giver and receiver effects (giver = 16% receiver = 6%). This suggests that in Longa there were greater inequalities, particularly in who was giving away food.

Dyadic reciprocity can range from -1 (negative reciprocity) through to 1 (positive reciprocity). A value of 0 equates to an absence of reciprocity. In all three camps reciprocity was positive and significant (table 2). Ibamba and Longa exhibited similar levels of dyadic reciprocity (Ibamba = 0.64, Longa = 0.59). Dyadic reciprocity was very high in Masia (0.89). Though there is considerable difference in the levels of dyadic reciprocity, even the lowest of these suggests that households tend to share food with others who give food to them.

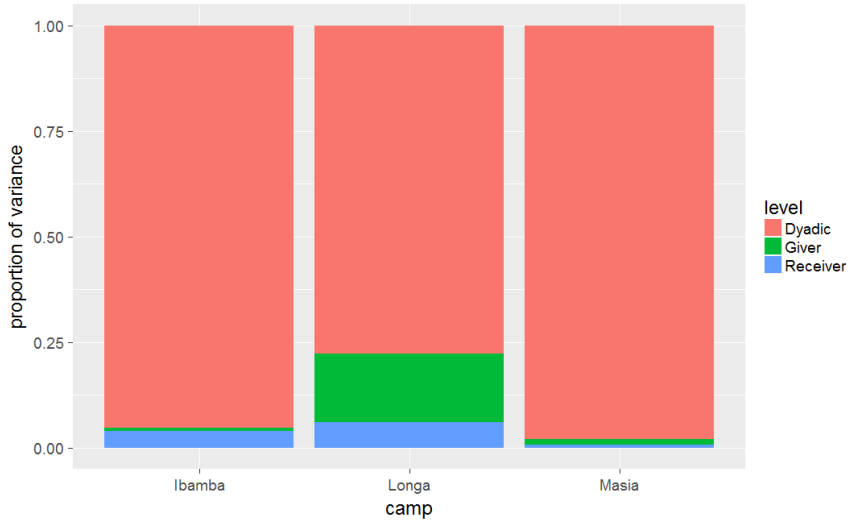

Figure 5.1. Proportion of variance in meal sharing at the relationship, giver and receiver levels for the three contemporary camps. (n - Ibamba = 156, Longa = 110, Masia = 56)

Table 5.2. Results from Intercept only SRM. Credible intervals are reported at the 95% level. Figures in bold represent effects whose credible intervals do not include 0 and are thus significantly different from 0. The Deviance Information Criterion (DIC) is used in Bayesian analyses for model comparison and can be interpreted in the same manner as AIC values. i.e. a reduction in DIC suggests an improved model.

Camp	Ibamba		Longa		Masia	
Households (dyads)	13 (156)		11 (110)		8 (56)	
	mean	credible intervals	mean	credible intervals	mean	credible intervals
β0 Intercept	0.36	-0.74 – 1.62	0.38	-1.27 – 1.74	**4.56**	**3.72 – 5.32**
Giver variance	0.39	0.00 – 2.28	**12.11**	**1.59 – 50.47**	0.28	0.00 – 1.50
Receiver variance	1.77	0.00 – 9.55	4.43	0.00 – 18.77	0.18	0.00 – 0.9
Relationship variance	**43.35**	**30.8 – 60**	**57.66**	**35.5 – 94**	**23.12**	**12.4 – 39.3**
Dyadic reciprocity	**0.64**	**0.47 – 0.78**	**0.59**	**0.34 – 0.82**	**0.89**	**0.78 – 0.95**
DIC	704.54		358.06		415.28	

Table. 5.3 Results of SRM analysis on meal sharing data with fixed effects. Credible intervals are reported at the 95% level. Figures in bold represent effects whose credible intervals do not include 0 and are thus significantly different from 0. The Deviance Information Criterion (DIC) is a Bayesian method for model comparison and can be interpreted in the same manner as AIC values. i.e. a reduction in DIC suggests an improved model.

Camp	Ibamba		Longa		Masia	
Households (dyads)	13 (156)		11 (110)		8 (56)	
	mean	credible intervals	mean	credible intervals	mean	credible intervals
β0 Intercept	0.95	-0.45 – 2.59	-7.94	-11.03 – -3.82	2.49	1.30 – 4.16
β1 distance	**-0.04**	**-0.06 – -0.02**	**0.15**	**0.06 – 0.24**	-3.63	-8.33 – 0.36
β2 kinship	**16.38**	**12 – 19**	**19.32**	**12.04 – 23.51**	-0.71	-3.12 – 2.03
Giver variance	0.48	0.00 – 2.21	2.05	0.00 – 8.16	**4.03**	**0.02 – 18.95**
Receiver variance	**5.01**	**1.19 – 12.45**	**11.22**	**2.32 – 8.16**	0.94	0.00 – 4.17
Relationship variance	**18.92**	**13.3 – 26.3**	**38.26**	**23.6 – 59.6**	**24.76**	**10.8 – 50.2**
Dyadic reciprocity	**0.38**	**0.17 – 0.62**	**0.25**	**0.09 – 0.48**	**0.82**	**0.50 – 0.96**
DIC	709.58		355.41		411.34	

Model including fixed effects

On inclusion of distance and kinship in the model, the DICs for both Longa and Masia were reduced in comparison to the intercept only model (Longa = 358 – 355, Masia = 415 – 411). The DIC was increased for Ibamba (705 –710) suggesting that in this case the fixed effect model performs worse than the intercept only model. Distance is negatively associated with food shared in all both Ibamba and Masia, though significantly only in Ibamba (table 3). This means that the closer two households are located, the more food they share. Kinship is positively associated with food sharing in both Ibamba and Longa. In Masia kinship was non-significant suggesting that in this camp more closely related dyads do not share more food than unrelated dyads.

Comparing relationship variance between the intercept only and fixed effect model shows that (43.35-18.92)/43.35 =0.56, or 55% of relationship variance in Ibamba is explained by distance and kinship. For Longa this is (57.66- 38.26)/57.66 = 0.34, or 34% of relationship variance and (12.11-2.05)/12.11 = 0.83, 83% of giver variance.

Comparing dyadic reciprocity between the models reveals considerable decreases in Ibamba (0.64 to 0.38) and Longa (0.59 to 0.25) when distance and kinship were included in the model. Masia showed only a small decline dyadic reciprocity on inclusion of the fixed effects (0.89 to 0.82). Thus much, but not all, of the reciprocal sharing in Ibamba and Longa occurs between neighbouring households and kin.

Kitanishi's data

Intercept only model

The data provided by Kitanishi provides a unique opportunity to compare a single camp in two different periods. The relatively small differences between the two periods (table 4)

suggest that patterns of meal sharing have a relatively high level of stability. There is a positive correlation between the amount of food transferred between specific household pairs in both periods (QAP correlation results; r = 0.57, SD = 0.08, p = 0.0002). During both periods, giver and relationship random effects were significant but receiver effects were not. The major difference between the two periods was in the proportion of variance at the giver level. VPCs for period 5 were - giver = 30%, receiver = 5%, relationship = 65% and for period 6 – giver = 47%, receiver =2%, relationship = 51%. As there were no changes in composition of group between these two periods this cannot account for the greater giver effect in the latter period. It is possible that shifts in ecology account for this difference, though both periods fell within a single rainy season. An alternative explanation is that some factor not reported by Kitanishi, such as illness, impacted upon one or more of the members of the group leading to a provisioning or care which we cannot take account of. Finally the difference in giver effect may just fall into the natural levels of variation.

Dyadic reciprocity was extremely high in both periods suggesting that the amounts of food received and given are closely correlated, taking into account the significant giver effect.

Model including kinship

Kinship is non-significant in both periods and has little impact on the amount of variation explained at any of the levels. Inclusion of kinship leads to a slight improvement in the model for period 5 (DIC 503.87 – 502.13) but the model performed less well than the intercept only model in regards to period 6 (DIC 602.04 – 603.12). Inclusion of kinship had no real impact upon the level of dyadic reciprocity.

Table. 5.4 Results of SRM for M group. Credible intervals are reported at the 95% level. Figures in bold represent effects whose credible intervals do not include 0 and are thus significantly different from 0. The Deviance Information Criterion (DIC) is a Bayesian method for model comparison and can be interpreted in the same manner as AIC values. i.e. a reduction in DIC suggests an improvement to the model.

Intercept only model

Camp	period 5		Period 6	
Households (dyads)	17(136)		17(136)	
	mean	credible intervals	mean	credible intervals
β0 Intercept	-1.22	-1.86 – -0.66	-0.69	-1.26 – -0.20
Giver	**0.76**	**0.19 – 1.96**	**0.89**	**0.28 – 2.23**
Receiver	0.12	0.00 – 0.53	0.04	0.00 – 0.21
Relationship	**1.63**	**0.86 – 2.78**	**0.98**	**0.57 – 1.56**
Dyadic reciprocity	**0.99**	**0.96 – 1.00**	**0.99**	**0.93 – 0.99**
DIC	503.87		602.04	

Fixed effects model

Camp	Period 5		Period 6	
Households (dyads)	17(136)		17(136)	
	mean	credible intervals	mean	credible intervals
β0 Intercept	-1.29	-1.97 – -0.70	-0.72	-1.28 – -0.20
β1 kinship	1.45	-0.50 – 3.36	0.88	-0.98 – 2.69
Giver	**0.82**	**0.23 – 2.05**	**0.89**	**0.27 – 2.12**
Receiver	0.15	0.00 – 0.59	0.04	0.00 – 0.20
Relationship	**1.60**	**0.84 – 2.78**	**0.97**	**0.56 – 1.57**
Dyadic reciprocity	**0.99**	**0.95 – 1.00**	**0.99**	**0.93 – 0.99**
DIC	502.13		603.12	

5.4 Discussion

Variation of the contemporary camps

In the previous chapter, I showed that meal sharing follows a similar form across all three study sites. This superficial similarity belies the complex web of interactions which constitute sharing in these camps. That being said, there are similarities between the three. In all camps most of the variance in meal sharing is at the relationship level. People do not share in a generalised or random way. Whether through choice or some other force, food tends to flow between specific pairs of households. In this way my data is similar to that reported from a horticulturalist village in Nicaragua (Koster & Leckie 2014), but differs markedly from the Venezuelan Ye'kwana (Koster et al. 2015), the only other group on which similar data areavailable. Considering the body of literature which shows high levels

of dyadic reciprocity and/or kin directed sharing (Gurven 2004, Ziker & Schnegg 2005, Nolin 2010), it is unsurprising that sharing occurs between specific sharing partners. What is more surprising is the difference between the camps. Whilst giver and receiver effects are almost absent from two of the camps (Masia and Ibamba) in Longa 22% occurs at the household level (16% giver and 6% receiver). The fact that controlling for relatedness and proximity lead to a large decline in variance at the giver level suggest that the "generous" households are sharing with kin and receiving less in return, suggestive of kin selected sharing. Masia comprised relatively few related households, explaining why kinship was non-significant for this camp and why a similar giver VPC is not observed. It is less clear why Ibamba does not exhibit the same giver effect as Longa, but is probably a reflection of a few households in Longa with relatives distributed widely throughout the other households of that camp.

My results suggest two factors in relation to reciprocity and meal sharing. Firstly, it is fairly high, suggesting that many if not all sharing partnerships are bidirectional, if not exactly equal in their transfer. Secondly, I show that there is considerable variation in the degree of reciprocity. From Masia, where the correlation is extremely high suggesting considerable levels of equity compared to the more noisy levels in Ibamba and Longa. Frequently analysis on food sharing is based on a single camp or village, or else data are aggregated. These results, as well as similar analysis on the Agta (Smith et al. 2016), highlight the considerable variation between camps. Amongst the Agta the variation seems to be associated with stability of camps, with those camps with slower rates of migration in and out of the group having higher levels of reciprocity (Smith et al. 2016). We do not have similar data for the Mbendjele, though all three camps appeared to exhibit low levels of stability, undergoing frequent shifts in membership throughout the study period. Assuming

mobility is not the explanatory factor in this case, what else may contribute to this difference? The population structure of Masia, in particular the networks of relatedness, may account for this difference. Of the 28 household dyads in this camp, 23 were unrelated. If reciprocal sharing and kin provisioning are occurring independently, then the latter would reduce the overall levels of reciprocity, given that it is likely to have unidirectional bias. Alternatively, sharing between kin may still constitute a form of reciprocal altruism. However, kin provisioning, independent of other forms of food sharing and kin biased reciprocity have both received some support (the former in Hooper et al. 2015 and Dyble et al. 2016; the latter in Allen-Arave et al. 2008, Nolin 2010 and Koster & Leckie 2014). In this case our results provide greater support for kin provisioning than kin biased reciprocity. Whilst Masia provided relatively few related dyads, those present were primary kin, mostly adult siblings. These are the types of family we would expect to engage in kin biased reciprocity rather than provisioning as they are likely to experience similar levels of shortfall, given that siblings are likely to exhibit considerable overlap in the period that they are raising family. The multigenerational kin dyads present in the other camps are where we would expect to see kin provisioning, with some households likely to be producing surplus and others at a deficit.

An alternative explanation for the greater level of reciprocity in Masia may relate to ecology. Hunting productivity, and consequently the proportion of meat in the diet, was far higher in Masia than the other camps (see chapter 4). Previous reports on food sharing have suggested that meat is more commonly and widely shared than other food types (Kaplan et al. 184, Kitanishi 1998). Given that meat is both high value and high variance this make sense. However, in this case food sharing does not appear to be more common in Masia (chapter 3, table 3), only more equitable. It is not obvious how a greater amount of

meat in the diet could impact on levels of reciprocity but not affect frequency or depth of sharing.

Differences in past and present meal sharing

Before I go on to discuss differences between the meal sharing reported by Kitanishi (1998) and my own data; it is worth considering these results in the context of previous publications which have made use of this data. Kitanishi's own analysis of the data stressed producer control and a preference for sharing with kin but failed to discuss reciprocity. Subsequent analyses have looked at the data in a cross cultural context, highlighting a high degree of reciprocity even compared to other hunter-gatherers (Gurven 2004, Jaeggi & Gurven 2013). Interestingly, previously calculated levels of reciprocity (Gurven 2004 = 0.6, Jaeggi & Gurven = 0.56 – 0.76) were considerably lower than those reported here (0.99). This stresses the importance of methods such as SRM which can take into account independent giver, receiver and relationship effects.

The meal sharing data collected by Kitanishi (1998) differ from my own in two ways; they reveal a large giver effect that does not interact with kinship and a higher degree of dyadic reciprocity. Whilst in Longa the giver effect disappears when controlling for relatedness, the larger giver effect of M group (Longa = 16%, M group = 30% (period 5),45% (period 6) is unaffected. Who are the "generous" individuals in M group and why does this effect not appear in the contemporary camps? In part this may result from differences in methods. The total number of meals observed in either period for M group was considerably smaller than either Ibamba or Masia, where each household was observed for 36 hours, and about equivalent to the number observed in Longa (table 1.). The difference in rate of meals observed suggests, understandably, that ad lib sampling of M group captured only a subset of meals. If this sampling were in any way biased so that certain households were observed

cooking more frequently than others, this could account for the giver effect I find. The number of meals observed in M group correlates strongly with the number of portions shared (Pearson's correlation $r(32) = 0.85$, $p < 0.0001$). Based on the published data, it is impossible to tell whether the skew in meals cooked is a product of sampling bias or a true representation of differences in productivity. Fortunately, by isolating the giver effect the SRM allows us to control for biases in sampling when we consider relationship level effects. As such, we can more reasonably suggest that the greater dyadic reciprocity in M group than in the camps observed in the present study is a product of ecological differences.

The apparent absence of kin-provisioning could account for the greater levels of reciprocity in M group, as I have argued it does for Masia. However, unlike Masia the structure of relatedness in this camp is more regular; with numerous kin ties at 0.5, 0.25 and 0.125 levels. Without more detailed demographic data, particularly in regards to children, it is difficult to see whether those kin ties where we would expect to find kin provisioning, such as grandmother-grandchild dyads, are present. But given that M group contained numerous examples of adult children living with their parents, this seems likely to have occurred. If we make the assumption that such kin ties were present, then why weren't relatives engaging in the type of sharing observed in Ibamba and Longa?

One explanation is that kin provisioning only becomes viable under relatively predictable conditions. Large, predictable life history related shortfalls require a sustained buffering strategy. Even the relatively brief critical period proposed by Marlowe (2003), the time from the birth of a child to 1 year of age at which Hadza women were shown to be significantly disadvantaged, clearly would require some consistent form of help. Elsewhere, it has been suggested that women remain at a calorific deficit until their mid-forties (Ache) or throughout their lives (Hiwi) (Hill & Hurtado 2009). Provisioning for these extended

periods represents a considerable inequality over time, requiring the provisioner to consistently acquire more calories than they consume. Reliable, calorie dense resources such as cultigens may allow for this in ways that wild foods do not. This raises the possibility that the provisioning we observe in contemporary Mbendjele, but also in the Agta (Dyble et al. 2016) and Tsimane (Hooper et al. 2015), could be associated with access to reliable sources of calories.

Conclusion

Meal sharing by the Mbendjele occurs between both kin and non-kin. I provide tentative support that sharing between these different groups may provide different functions. Sharing between kin may represent investment in inclusive fitness via provisioning, whilst sharing between unrelated households constitutes a form of direct reciprocity as a means of buffering risk. The relatively large giver VPC in Longa, and the lower levels of reciprocity in Ibamba and Longa, suggest that sharing between kin is not entirely balanced. When sharing between kin is largely absent, as in Masia, extremely high levels of reciprocity are observed, suggesting that sharing is contingent on past interactions and/or expectations of future reciprocation.

Kinship provides some explanation of sharing among the Mbendjele but it is clear that it is not the only factor at work. Relatedness and proximity explain only about half of the relationship variance in meal sharing in Ibamba and Longa and almost none for Masia. Neighbours and kin are often the preferred sharing partners, but transfers also frequently occur across these boundaries. In the following chapter I look at what other factors could affect partner choice by comparing meal sharing to other Mbendjele social networks.

6. Mbendjele social networks and their impact on sharing

In chapters 4 and 5 I examined the extent to which Mbendjele sharing is a product of dietary variance and tested which of the major ultimate explanations for cooperation - reciprocal altruism and kin selection - better explains the behaviour. The previous chapter showed that the majority of variation occurs at the level of the relationship between sharing partners and that kinship and proximity account for only a small amount of this variance. In this chapter I examine how other social relationships interact with sharing. I first discuss the application of social network analysis and remote sensing technologies in the construction and analysis of naturally occurring networks. To assess the uses of different network types, I compare proximity networks, collected via motes, with association networks, collected via observation. I then analyse how proximity and association networks interact with food sharing. I first test whether an individual's position within these networks impacts the amount of food they give and receive. I then examine whether social ties predict sharing at the dyadic level. The results reveal that network position has relatively little impact on sharing, but that social ties do facilitate the transfer of food.

6.1 Introduction

The structure of this thesis has loosely recapitulated the trajectory of food sharing studies over recent decades. Early work focussed on the specific form of the behaviour, examining how much and what types of food were shared (Kaplan & Hill 1985, Bahuchet 1990, Kitanishi 1994). Focus then shifted to look at the relationships between those who share, using similar analyses as to that in the previous chapter (Gurven et al. 2001, Ziker & Schnegg 2005, Allen-Arave et al. 2008, Nolin 2010, Koster & Leckie 2014, Koster et al. 2015). The unit of interest changed from the individual to the dyad. To analyse dyadic data,

many of these studies have drawn on social network analysis (SNA), utilising techniques such as quadratic assignment procedures (Ziker & Schnegg 2005) and exponential random graph modelling (Nolin 2010 & 2012). Far from being restricted solely to food sharing studies, the last decade has seen a rapid expansion in the application of SNA to behavioural ecology (Krause et al. 2007, Sih et al. 2009). SNA provides new ways to describe social structure (Dyble et al. 2016), the ability to quantify and measure the impact of sociality on fitness (Brent 2015, Salali et al. 2016) and provides a framework to examine polyadic processes, such as the transmission of information and disease (Rimbach et al. 2015). Contributing to the rising popularity of SNA have been improvements in sensing technologies. Where previously collection of network data required a considerable investment of time, particularly in natural settings, improvements to technologies such as GPS and RFID mean that such data can be collected with relative ease (Leu et al. 2010, Salathre et al. 2010, Vazquez-Prokopec et al. 2013).

The major application of SNA to food sharing studies has so far largely been methodological, providing tools for handing and analysing dyadic data (Ziker & Schnegg 2005, Nolin 2010 & 2012). The main theoretical insight of SNA, that people and interactions beyond an individual's immediate social environment can impact upon them, has received little attention in regards to sharing. Recent work on the Mbendjele and Agta has suggested that the overall structure of sharing networks may provide new information on the function of food sharing (Dyble et al. 2016). Somewhat analogously, a recent paper on Tsimane exchange has sought to analyse food sharing within a wider social context (Jaeggi et al. 2016).

As well as applying network analysis to sharing directly, SNA provides us with new ways of comparing and correlating food sharing with other social networks. In the previous chapter,

I found evidence of partner choice in Mbendjele food sharing. Whilst kin and neighbours explain some of the variance a large component of the relational variance remains unexplained. Work on the food sharing of South American horticulturalists has found large "association" predictors (Koster & Leckie 2014, Koster et al. 2015). People who spend a lot of time together and interact frequently also tend to share more food. This perhaps suggests that just like kin, associates are favoured sharing partners. An alternative explanation is that relational wealth can be used to gain greater access to food sharing. For the Mbendjele discussed in this thesis, increased relational wealth, measured using a simple gift giving game where individuals were asked to nominate other camp members to receive a gift of honey, was found to correlate with a greater number of food sharing partners (Chaudhary et al. 2016).

In this chapter, I examine the relationship between the meal sharing and other social networks. I first compare two social networks - proximity and interaction networks - and assess how both can be used. I then compare sharing networks to these other network types in order to assess the impact of sociality on food sharing.

6.2 A comparison of Mbendjele proximity and interaction networks

Networks are formed of two components, nodes - the individuals or actors, and edges - the ties between these nodes. For social networks, nodes will typically be the individual people or animals within the population, though in this chapter households are also considered as nodes. Edges may represent any number of different interactions and can be binary, where an edge is either present or absent, or weighted. The edge variable may highly specific, for instance donations in a gift giving game (Apicella et al. 2012) or on the amount of food shared between people (Ziker & Schnegg 2005), producing specific sharing networks. An

alternative approach is to measure a range of interactions and combine these into a single social interaction index (Kaspar & Voelkl 2009, Koster and Leckie 2014, Koster et al. 2014).

A third possibility is to measure all interactions between a dyad, categorize each interaction into separate networks and then compile multiple networks into a multidimensional social network (Barret et al. 2012). This attempts to capture the true and complete social network of a group, whilst the two former methods, which represent most studies, use the term "social network" as a broad umbrella, inclusive of a range of different networks which may vary considerably. If taking this third approach, a researcher wishing to use SNA to study a specific group is faced with the question of which type of social network to study. In an ideal situation, the edge measurement should be chosen based purely on the theoretical questions being addressed.

Studies of contagious disease are one area in which SNA has proven a highly valuable tool and serve as a clear example of how the social network needs to be chosen based on the specific subject. For example, a study on the social networks of spider monkeys (*Ateles hybridus*) found that ties in a physical contact network were more important in the transmission of parasites than proximity network ties (Rimbach et al. 2015). Studies of infectious disease provide a clear of example of how important it is to consider the type of social network used after considering the means of contagion. This same level of scrutiny needs to be applied to all work which utilises SNA. Ideally where the question being addressed relates to social support, a network based on this type of interaction should be used. If the subject of interest is information transmission then a network based on communication may be more appropriate.

Unfortunately, such theoretical considerations are not the only factors affecting which social networks can be constructed. Practical constraints also play a role. This is particularly

the case when constructing networks for natural populations of both humans and non-human animals. By and large SNA requires data on the entire network population. Whilst it is possible to measure an individual's direct social network and individual measures such as in-degree by just observing that one individual, global network measures such as density and clustering and even individual level metrics such as centrality can usually only be calculated if all nodes in the network have been observed or interviewed. SNA is an area of continued and rapid development and methods, which make use of or account for partial networks, where only a sub-sample of the nodes have been observed, are able to provide some information (Silk et al. 2015). However, at present such analyses are relatively limited in in comparison to analyses on complete networks.

Consequently, most studies utilising social networks attempt to capture a complete network. This can mean a considerable investment of time and effort in order to collect all the data. In the study of human social networks this can be circumvented through the use of interviews and experiments rather than actual observation of social behaviour (Apicella 2012). This allows data to be collected on large samples in relatively brief period of time. Such methods are highly efficient; however interviews also have a significant limitation. Interviews allow the construction of networks based on perceived social ties rather than on actual interactions and are likely to be more appropriate for answering certain questions rather than others.

Perceived networks are clearly a subject worthy of study but provide an alternative to interaction networks rather than a replacement, both are able to produce insight not reachable using the other network type. Furthermore, interviews are not always possible or appropriate. Clearly for biologists working on non-human animals, such methods are not available and it is necessary to undertake the time-consuming process of observational

data collection. However, advances in technology have greatly increased the efficiency with which data can be collected. The increasing ease of use, reliability and reduction in cost of technology such as GPS (Leu et al. 2010, Vazquez-Prokopec et al. 2013), motes (Salathre et al. 2010), RFID (Stehle et al. 2011), radio tracking (Perkins et al 2009) and even acoustic sensors (Guttridge et al. 2010) have led to their rapid adoption in studies of both humans and non-human animals. These technologies allow the collection of high resolution data, often on a large number of individuals simultaneously and are being rightly adopted by researchers. Such data can then be used to construct a proximity network for the group, wherein the edge weight is the amount of time that two actors spend within a set distance of one another. The use of proximity networks did not come about with the adoption of tracking technologies but they have been utilised by biologists for as long as SNA (Croft et al. 2004). Proximity networks can been used in two distinct ways, either directly looking at how proximity patterns relate to other aspects of an individual's behaviour and fitness, or as an analogue for other types of social network. Proximity data are relatively easy and quick to collect, and sensing technology has dramatically increased this advantage. However, this raises the question how suitable proximity is as a proxy for other social behaviour?

The association between proximity and sociality is not straightforward. The majority of social interactions require the actors to be in relatively close proximity, but the behaviour of modern humans aided by communications technology and the infrasound calls of elephants (McComb et al. 2003) are notable exceptions. However the use of proximity as an analogue for other social behaviours is hampered on two fronts. Firstly not all proximity is social, actors can find themselves close to another individual as the result of external factors and stochasticity. A second limitation of proximity data is that it aggregates many

social behaviours into a single measure. For example, it does not discriminate between antagonistic and affiliative interaction. Work on Barbary macaques (*Macaca sylvanus*) showed, that contrary to what we might expect, position within an antagonistic network is a better predictor of survival than affiliative network position (Lehmann et al. 2016). In this case, use of a simple proximity measure would probably have been interpreted as evidence for the more expected hypothesis, that affiliative social interaction increases survival chances.

The use of proximity as a proxy for other social interactions is contingent on a close correlation in the properties of the networks. I test whether this is the case for the Mbendjele BaYaka by comparing features of a proximity network with the same features of an interaction network.

SNA allows the quantification of social data in a large variety of ways, producing metrics at an individual, local and global level. Global metrics give an idea at to the size and form of the overall network. For instance, we can calculate the density of edges, the diameter of the network and the extent to which the network can be divided into distinct clusters. Local network metrics can provide information on an individual node's involvement in the network. A node's degree is simply the number of other nodes with which it shares an edge. Strength is the summed weight of all of a node's edges, effectively quantifying ego's total investment into the network. Furthermore individual level metrics can provide insight into a nodes position within a network. Often such metrics are referred collectively as centrality measures and can be thought of as highlighting which nodes are more central in the network and which are more peripheral. Unlike degree and strength, calculation of centrality measures requires the wider network be considered, including edges unconnected to the ego.

6.2.1 Methods

Constructing networks

Three types of social network are analysed in this chapter (Table 1). Sharing networks were constructed based on the same dyadic data analysed in the previous chapter. Thus each node represents one of the households in the camp and edges represent the total amount of food (in Kcal) transferred between each household-household pairing. Sharing networks are directed as food transferred from *ij* and that transferred from *ji* are both used in its construction. Proximity networks were constructed from data collected by the motes (full details of the mote data collection can be found in chapter 3). Each node represents a single individual adult in the motes sample. Edge weights are calculated as the proportion of the total time two individuals were both resident that they spent within 3 metres of one another. This was calculated by dividing the recorded "beeps" for *ij* by the total number of potential beeps for *ij*. Thus the proximity networks are weighted but undirected as *ij* = *ji*. Interaction networks were constructed from scan observation data.

Table 6.1. Details of the three types of social network and the methods used to construct them.

Network type	Node	Edge weight	Data collected via
Sharing	Household	Calories transferred from *i* to *j*	Focal observation
Proximity	Individual	Proportion time *ij* were within 3 metres of one another.	Motes
Interaction	Individual	Proportion of shared scans in which *ij* interacted	Scan observation

Table 6.2. Explanations of the network measures used

Statistic	Definition
Eigenvector centrality	A measure of a nodes influence in a network. Each node is given a score depending on how well connected that node is. A node with high eigenvector centrality is connected to high scoring nodes.
Betweeness	A measure of how important a node in a network is as a link between other nodes. It is calculated as the number of shortest paths through a network between all potential dyads which pass through the node of interest.
Flow	A second measure of betweeness which uses all paths between dyads, not just the shortest, and calculates the proportion which pass through the node of interest.
Freeman's out degree	A measure of the number of direct connections a node has.
Inverse weighted degree	A measure of the number of direct connections a node has weighted by the strength of the connections.

Analysis

I compare the proximity and interaction networks in two ways. Firstly, I compare dyadic measures of proximity and interaction to see to what extent they correlate, i.e. examining to what extent those pairs who interact often are also in close proximity. Secondly, I compare a range of network statistics calculated for each node across the two network types. This allows us to assess whether people hold similar position in the two different networks.

As the data are dyadic and each individual appears in the data set multiple times analyses need to account for pseudoreplication. Quadratic assignment procedures (QAP) allow the calculation of standard correlation and regression coefficients whilst accounting for the non-independence of dyadic data via random permutation of the data. The QAP occurs in two stages. Firstly, a standard correlation or regression coefficient is calculated from corresponding cells in two adjacency matrices. Following this the columns and rows of one of the matrices undergo simultaneous random permutation after which the test statistic is recalculated and stored. This random permutation occurs multiple times. The proportion of random permutations in which the test statistic was greater than that of the original

unpermuted data is calculated and serves as a p value. To examine the extent to which dyadic measures of proximity and interaction correlate I performed a Pearson's correlation QAP test on the proximity and interaction networks for Ibamba. The data underwent 5000 permutations and the QAP was performed in UCINET (Borgatti et al. 2002).

To compare network position between proximity and interaction networks a number of node level statistics were calculated in UCINET (Borgatti et al. 2002) (table 2). Kendall's rank test was then used to assess the extent to which those who scored highest for each statistic for the proximity network also scored highly for the interaction network.

6.2.2 Results

Measures of proximity correlate with interaction

To see how well a dyad's measure of proximity correlated with interaction a QAP correlation was performed on the two matrices in UCINET with 5000 permutations of the matrices occurring. The two measures were significantly positively correlated (Pearson's correlation r= 0.36, p=0.01). Thus the more time ego spends in close proximity to someone the greater the likelihood ego interacts directly with them. However, the relatively low coefficient clearly suggests that proximity and interaction are not the same thing and whilst the latter requires the former, for the Mbendjele, the reverse is not true.

Individual's local proximity and interaction networks are similar.

The degree of a node allows us to gauge how much an individual invests in social interactions. Degree measures show the number of ties, the strength of all ties combined, or a combination of both. I calculated two degree measures, Freeman's degree and inverse weighted degree, for both the proximity and interaction network. All network statistics were calculated in UCINET (Borgatti et al. 2002). The statistics were then compared using

Kendall's rank tests. Both degree measures were positively correlated between proximity and interaction networks (Table 2.) Thus, if our intention is to gauge which individuals spend the most time involved in social interaction or with the most people proximity, serves a good proxy for actual interactions.

Individual's position within a proximity network differs from position within an interaction network.

As well as looking at the direct interactions of an individual node, SNA allows us to see how those nodes are situated within the wider network. Of particular importance are measures of centrality. These quantify how well connected a node is by, not only looking at their direct links, but also looking at the social ties of their partners and so on. I calculate and compare three centrality measures for the proximity and social networks, eigenvector centrality, flow and betweeness. Again, I used Kendall rank tests to assess the correlation between the two network types. Eigenvector centrality was positively correlated between the two networks (table 3). Neither flow nor betweeness were correlated. A high eigenvector centrality means that the ego is connected to well-connected nodes. Thus in the case of the interaction network those nodes with a high eigenvector centrality score interact with people who themselves are investing relatively highly in these interactions with other people.

In light of the dyadic correlation between interaction and proximity it is not surprising then that those with high eigenvector scores in one network also have high scores in the other. Both betweeness and flow are measures of how many paths through the networks route through ego. Nodes which score highly for these measures may act as bridges connecting up relatively isolated components. The lack of correlation for both of these measures across proximity and interaction networks means that the important bridging nodes on one

of these networks were not the same as the in the other, despite the correlations in the other measures already reported.

Table 6.3. Kendall's rank correlation coefficients of individual network metrics calculated for interaction and proximity networks. Figures in bold indicate a significant correlation (p < 0 .05). N = 20.

Statistic	coefficient	p value
Eigenvector centrality	**0.40**	**0.015**
Flow	0.10	0.536
Betweeness	0.18	0.267
Inverse weighted degree	**0.48**	**0.006**
Freeman's out degree	**0.39**	**0.018**

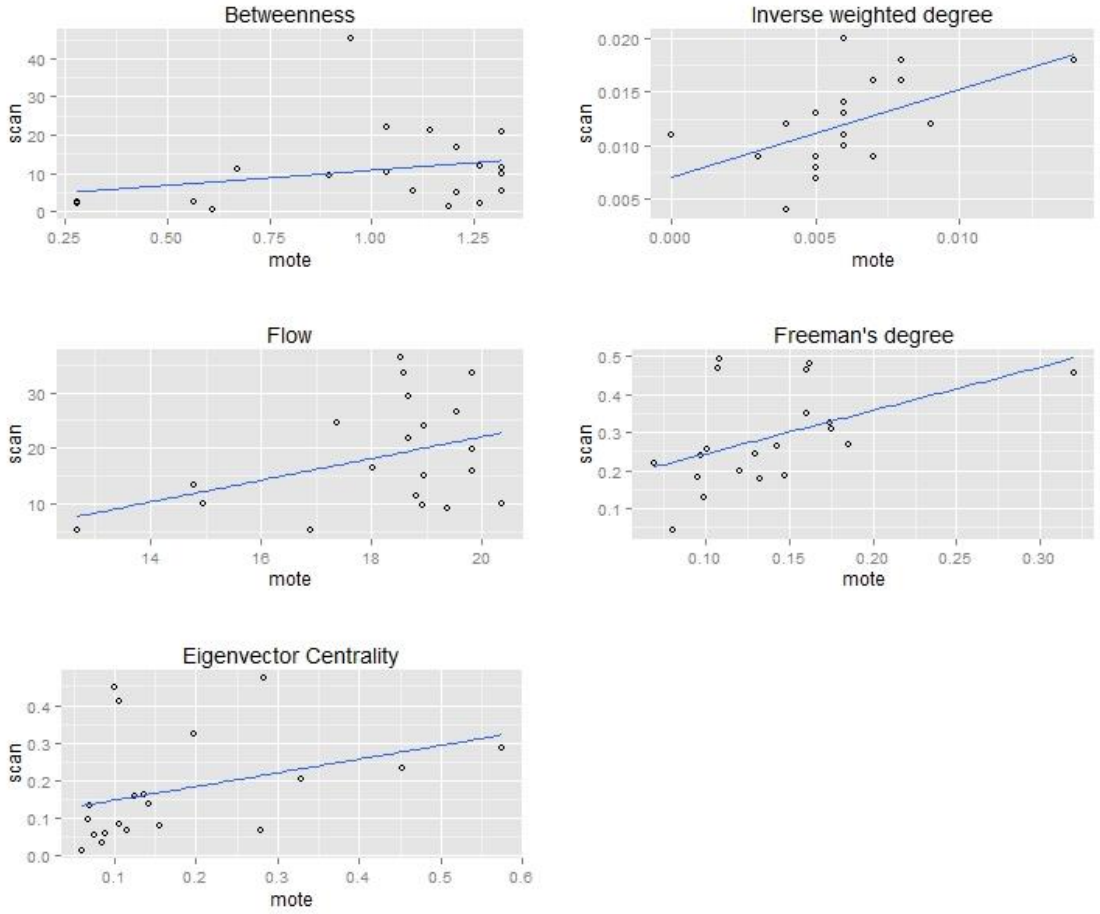

Figure 6.1. Plots of individual metrics from the proximity network (scan) against the same metric from the interaction network (mote) (N=20).

6.2.3. Discussion

Clearly proximity and interaction are closely associated. Unlike in industrial societies where these two associations have to some extent become divorced, amongst the BaYaka the latter still requires the former. By measuring proximity it appears there are several things we can predict about an individual's behaviour and local interaction network. The fact that dyadic measures of proximity and interaction correlate means that proximity can provide useful data for addressing a range of questions regarding an individual's direct interactions. Questions such as 'do people associate preferentially with kin or within the same age group?' can be answered using proximity data and then generalised to a broader category of social behaviour. Similarly, the correlation between an individual's local proximity and interaction networks suggest that, in the case of the BaYaka, it is possible to use proximity data to address questions such as which individuals are investing more in sociality. Such data can then be combined with information on health and reproductive outcomes in order to look at the fitness costs and benefits of sociality.

However, these results highlight the fact that despite all the similarities we cannot assume all network statistics are so closely related. Betweeness, of which I compared two measures, flow and Freeman's betweeness, did not correlate for proximity and interaction. These measures look not only at the direct links of a node as with measures of degree, or only one step away as with eigenvector centrality, but consider the overall shape of the network. A few extra edges in the network can alter the betweeness of all nodes whilst only the affecting degree and eigenvector centrality scores for a small sub set. This is clearly important methodologically whilst also raising some interesting theoretical questions.

As in a previous study on baboons (Castles et al. 2013), I find that proximity and interactions networks differ in some important ways. In particular, I find that it is at the

larger scale of network statistics and position of nodes within networks that these differences are most apparent. The fact that network level statistics such density and clustering differ is perhaps of most importance to comparative studies which attempt to compare networks of different populations or even different species. The fact that SNA allows us to quantitatively describe group level phenomena such as this is an obvious boon to comparative studies. However, often comparative studies will make use of data collected by different researchers using different methodologies and sometimes on completely different types of social network. Clearly the results presented here suggest that we should be sceptical of any conclusions drawn from this type of comparison. Comparative studies must attempt to match networks of the same type; proximity with proximity, grooming with grooming, if they seek to really understand differences in sociality between species at the network level. Even when the same network types are used, care needs to be taken. Amongst baboons even different data collection methods of the same edge measurement produced quite different networks (Castles et al. 2013). Even in non-comparative studies, focusing on a single study population the results presented here serve as a note of caution. In this case proximity data can only address questions relevant to position within a proximity network and not within a more general social network. We must consider what it means to have high betweeness within a proximity network and the hypotheses being tested, and the conclusions drawn, should also reflect this fact. In the light of this it is worth considering when position within a proximity network is useful and what are the limits of this type of data for which we may need to construct networks of a different type.

Given these results we can assess how social network data can be utilised in regards to food sharing. In the following section, I first assess whether an individual's position within a

social network affects their involvement in food sharing. I then assess how an individual's local network interacts with sharing. Given the correlation between interaction and proximity networks in regards to degree and edge weight, either network would be appropriate.

6.3 Influence of social capital on sharing

The fitness consequences of sociality have been one of the central concerns of both evolutionary anthropology and primatology for several decades. Early work considered group living at a broad scale, often focussing on cross species comparisons to identify benefits such as predator avoidance and how these were traded off against increased competition from conspecifics (Crook & Gartlan 1966, Wrangham 1980). Increasingly a more granular approach has been taken, with researchers looking to identify the costs and benefits of specific focal behaviours on the actors directly involved. Social network analysis has allowed further refinement of this individual level approach whilst also serving as a bridge to work on social structure at a group level. Perhaps the largest contribution of SNA to our understanding of the fitness implications of sociality is in identifying situations in which the social interactions between a specific dyad can have effects on the fitness of all group members, even to those with whom they do not have direct contact. For example centrality has been shown to correlate with longevity in rock hyraxes (*Procavia capensis*) (Barocas et al. 2011) and clustering impacted on survival of Barbary macaques (Lehmann et al. 2016)

Social behaviours are many and varied, both within and between species; and unsurprisingly sociality can impact on fitness in various ways. Among female baboons, greater involvement in social interactions has been linked to both an increase in longevity (Silk et al. 2010) and higher infant survival (Silk et al. 2003) whilst for male Assamese

macaques (*Macaca assamensis*) strong social bonds were associated with greater paternity success (Schülke et al. 2010). Such patterns are not restricted to primates. For feral horses, sociality was associated with increased birth rate and infant survival (Cameron et al. 2009, Nunez et al. 2015). Amongst humans there is relatively little research looking at the benefits of sociality, beyond a burgeoning body of literature exploring the negative impact of social isolation on health (Hawkley & Capitanio 2015). It is then of some significance that amongst this population of Mbendjele relational wealth, measured using a simple gift giving game, wealth is associated with both higher female fertility and an increased number of sharing partners (Chaudhary et al. 2016). This raises the intriguing possibility that the Mbendjele can use social capital to gain better access to food. To examine the impact of sociality on food sharing I examine firstly whether an individual's position with a camp wide activity network influences their involvement in sharing. I then examine whether an individual's direct social ties influence sharing.

6.3.1 Methods

Network position

To assess the impact of social network position and social ties on meal sharing, I use the previously discussed activity network. I tested for correlation between proportion of a household's diet provided by someone outside of that household with three measures of centrality; eigenvector, betweeness and flow. Statistics were calculated for both the men and women of a household and tested separately, so that each household was included only once per analysis. Kendall's rank test was used and all analysis performed in R.

Influence of social ties on sharing

Multiple regression quadratic assignment procedures (MR-QAP) were used to examine the effect of social ties on meal sharing, defined as edge weight from the meal sharing network. Nodes for the meal sharing network are households, whilst for the activity network they are individual this required the transformation of the latter.

1. Male-male network - The strongest edge weight from the activity network between two adult men from household *i* and *j*.
2. Female-female network - The strongest edge weight from the activity network between two adult women from household *i* and *j*.
3. Male-female network - The strongest edge weight from the activity network between an adult man and an adult woman from household *i* and *j*.

Due to loss of data in Masia, resulting from faults in the motes, this analysis was performed for only two of the camps (Ibamba & Longa). For both camps, I report the results of seven models. Each of the predictors is first included on its own, the analysis is then repeated including relatedness as an additional predictor. Household-household relatedness is calculated in the same manner as the analysis in chapter 5. To briefly summarise, the coefficient of relatedness is the largest coefficient between any two members of the respective households. Coefficients less than 0.125 are treated as 0 in this analysis. A final MR-QAP model contains all three social networks and relatedness as predictors of food sharing.

Caveats and limitations

The activity network uses a single measure of interaction between the two parties. This was necessary as many behaviours occur only infrequently and were not observed for all dyads. I believe this is not truly representative of an absence of such behaviours for a particular dyad, but simply a reflection of the limited time that data collection occurred

over. Thus it was deemed not appropriate to create behaviour specific networks. One of the problems of the single measure interaction network is that it does not differentiate between affiliative and antagonistic interactions. Indeed, the same criticism can be levelled at the raw data, it was simply recorded that two individuals were speaking, divorced from the content and context of the conversation. It is reasonable to suggest that sharing is more likely between people who are friends rather than people who are frequently antagonistic and in an ideal world this would be accounted for in the analysis. In the absence of good measures of affiliation and antagonism, I believe that the single interaction measure probably serves as a decent proxy or the former rather than the latter. This is simply based on my time with the Mbendjele and the relative frequency of friendly conversation versus arguments. It is my belief that antagonistic interactions are relatively poorly represented in the scan data.

6.3.2. Results

In general measures of centrality in the interaction network do not correlate with the proportion of a household's diet provided by other members of the camp. Whilst positive trends can be observed (Figure 2), these do not reach significance with a single exception (Table 4). Whilst neither eigenvector nor betweeness correlated significantly with food received, flow did positively correlate for males. Whilst all other network metrics were non-significant it is interesting to note that correlation coefficients were higher for males across all network measures.

Table 6.4. Kendall's rank correlation coefficients between various measures of network position and proportion of diet from outside of household. Figures in bold indicate a significant correlation ($p < 0.05$).

Statistic	coefficient	p
male eigenvector	0.40007	0.1702
female eigenvector	0.26318	0.2571
male betweeness	0.28571	0.3988
female betweeness	0.06061	0.8406
male flow	**0.6429**	**0.0312**
female flow	-0.1212	0.6384

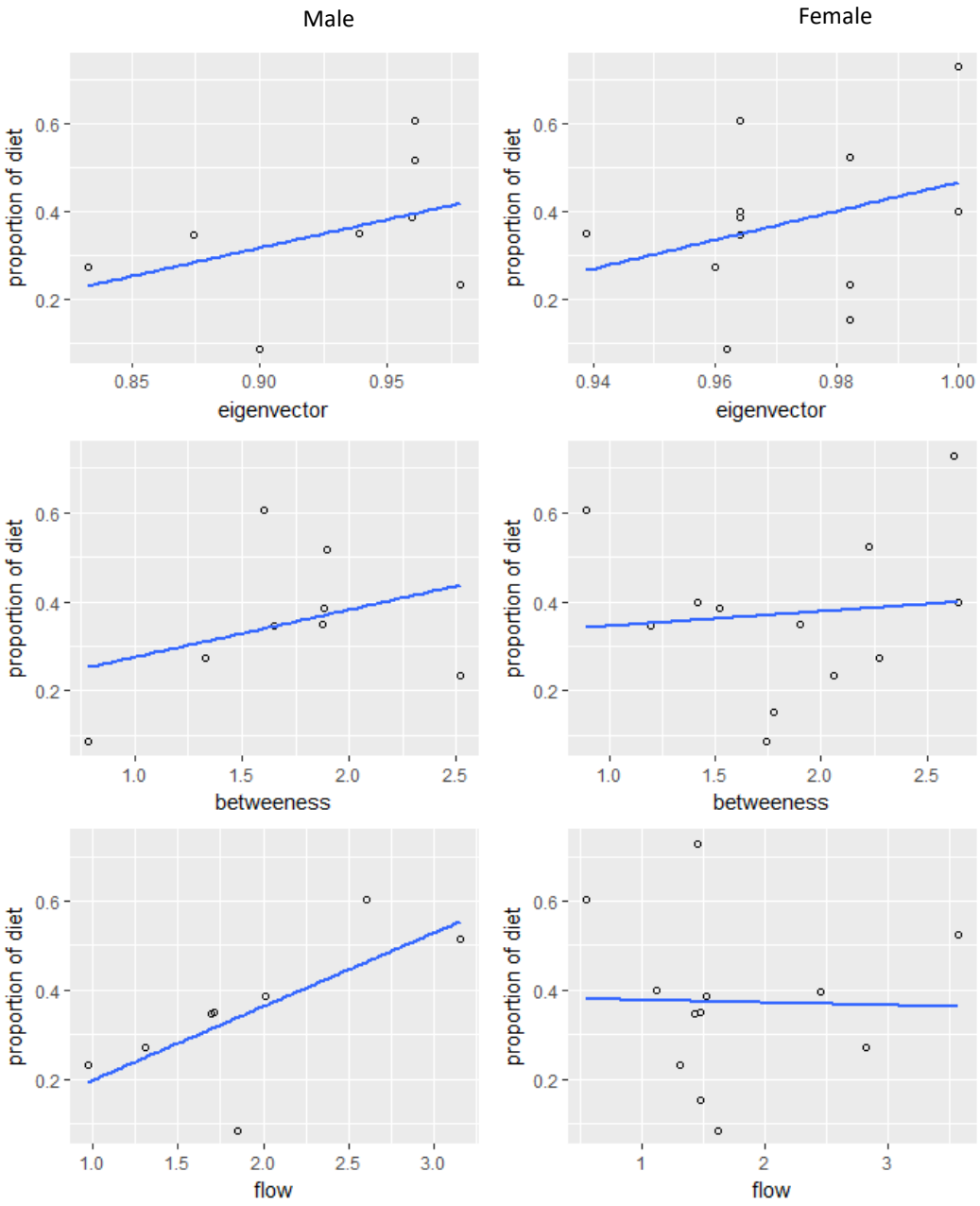

Figure 6.2. Correlations between proportion of a household's diet received from other households against various network statistics calculated from an activity network. Males on the left females on the right

Social ties and sharing

When included as the only variable, social ties positively predict food sharing (Table 5), with one exception. Male-male ties in Longa appear to have no impact on food sharing. In general, those people who interact more frequently also more frequently share food. Many "associates" are related and controlling for kinship leads to large decreases in the variance explained by association. This is particularly the case for Ibamba, though both male-male and male-female associations remain significant. In the full model for Ibamba, only male-female associations remain significant perhaps suggesting that the significance of male-male association was a result of a correlation between spouse's associates. In Longa controlling for relatedness had a much smaller impact upon association as a predictor. Both female-female and male-female associations were significant in all models. This suggests that these social ties both encourage the sharing of food independent of relatedness and each other. That being said, overall the models performed poorly for Longa. The best model (full model) explained under 20% of the variance in meal sharing ($R^2 = 0.17$, $p = 0.002$). In contrast the same model explained over half the variance in Ibamba ($R^2 = 0.54$, $p= 0.001$)

Table 6.5. Results of MRQAP tests with social ties and relatedness as predictors of meal sharing. Figures in bold are significant at the 0.05 level.

IBAMBA

Model	R^2	p	intercept	male-male	female-female	male-female	relatedness
male only	0.37	**0.002**	1.31	**0.62 (0.00050)**	NA	NA	NA
female only	**0.10**	**0.009**	3.60	NA	**0.32 (0.008)**	NA	NA
male-female only	**0.27**	**0.002**	5.14	NA	NA	**0.53 (0.001)**	NA
male & rel	**0.48**	**0.001**	-1.08	**0.37(0.012)**	NA	NA	**0.43 (0.012)**
female & rel	**0.42**	**0.001**	1.53	NA	0.01 (0.41579)	NA	**0.65(0.0005)**
male-female & rel	**0.49**	**0.001**	0.53	NA	NA	**0.32(0.0035)**	**0.52(0.0005)**
full model	**0.54**	**0.001**	-0.10	0.18015(0.16442)	-0.02(0.49825)	**0.37(0.03298)**	**0.42 (0.01699)**

LONGA

Model	R^2	p	intercept	male-male	female-female	male-female	relatedness
male only	-0.01	0.535	0.05	-0.01(0.522224)	NA	NA	NA
female only	**0.12**	**0.01**	-0.01	NA	**0.36 (0.00350)**	NA	NA
male-female only	**0.07**	**0.011**	0.02	NA	NA	**0.28 (0.012)**	NA
male & rel	**0.06**	**0.014**	0.02	-0.01(0.5)	NA	NA	**0.28(0.012)**
female & rel	**0.15**	**0.004**	-0.02	NA	**0.31 (0.009)**	NA	**0.19 (0.02749)**
male-female & rel	**0.12**	**0.004**	0.01	NA	NA	**0.25 (0.01349)**	**0.25(0.01299)**
full model	**0.18**	**0.002**	-0.03	-0.04 (0.34)	**0.28(0.015)**	**0.23(0.032)**	**0.17 (0.04398)**

6.3.3. Discussion

Food sharing networks are resilient to social manipulation

Whilst several studies have been able to link sociality with outcomes such as longevity, fertility and infant survival (Silk et al. 2003, 2010, Cameron et al. 2009, Schülke et al. 2010, Nunez et al. 2015), the proximate mechanisms of this relationship remain poorly understood. One potential pathway is that those individuals with greater social capital are more reliably able to draw directly upon the support of others. To test this hypothesis, I examined whether hunter-gatherers were using their position within a social network to gain greater access to resources held by other households. On the whole this does not appear to be the case. Those individuals positioned centrally in the interaction network are no more or less involved in sharing than those on the periphery. In truth, given what we know specifically about the sharing networks of the Mbendjele, this is not surprising. Food sharing appears to be a means of buffering against unpredictability in foraging returns, providing a source of food that can be drawn upon at times of shortfall. For such a system to be resistant to free riders and cheats the donation of food must be contingent on the expectation of future reciprocation. If it were possible to use social capital to gain access to food sharing this would be evidence of a lack of contingency. Whilst in general I find a little evidence for the influence of social capital influence on sharing there are several novel results which suggest that the picture is not completely clear cut.

Centrality is a broad term in social network analysis, covering various measures of a node's importance with a network. Whilst there is often considerable correlation between different centrality measures it is clear that they are distinct from one another and provide different insight into the functioning of a network and the position of nodes within it (Valente et al. 2008). Thus, it is not unexpected that certain centrality measures are better

at predicting involvement in sharing than others. But what does the fact that it is only flow betweeness that is significantly correlated with resource transfer tell us about sharing amongst the Mbendjele? Flow betweeness is similar to the more common betweeness measure, often referred to as Freeman's betweeness (Freeman 1979), also tested in this chapter. Where they differ is that Freeman's betweeness is based on geodesic (i.e. shortest) paths through the network, whilst flow betweeness is based on all independent paths (Freeman 1991). That either of these measures was significant is of interest as it implies that movement through the network is of importance and that those men who are situated at points of path convergence, for instance at a bridge point between two clusters, have more food directed towards their household.

The fact that men's social position has greater effect on sharing than women's is a novel result, though one which does not have an obvious explanation. One possible explanation is that, as a result of the division of labour, with women cooking the large majority of all food, men are rarely active donors in the meal sharing network. Thus, it is possible that those women who are socially well connected gain access to a greater amount of shared food whilst simultaneously being exposed to greater demand for sharing which effectively equals out. In contrast, well connected men may be able to put themselves in a position to acquire food without serving as a conduit of food sharing out of the household.

Social ties predict the transfer of food

The result that network position has relatively little impact on sharing is in accordance with the SRM analysis in chapter 5. If an individual's position strongly affected sharing, we would expect to find large giver and/or receiver effects. The large relationship effect, found for all camps, shows clearly that sharing occurs between specific pairings, raising the question of what factors are important in the formation of sharing partnerships. The analysis in chapter

5 showed that both kinship and proximity were two relationship traits which predicted sharing. The analysis in this chapter means we can add association to this list. A similar result has been reported for South American horticulturalists (Koster & Leckie 2014, Koster et al. 2015). It is important to consider whether such an effect is the consequence of partner choice or an emergent property of simpler sharing rules. If the former, we need to consider what the advantages of preferentially sharing with an associate are.

It is inherent to our measurement that associates are those people who spend more time together. This alone could account for the correlation between association and sharing. It should be noted that the same can be said for the kinship and proximity effects if, as seems likely, neighbours and relatives spend a greater amount of time with one another. Such exposure effects are an example of what Brosnan and De Waal (2002) refer to as symmetry based reciprocity. Unlike attitudinal or calculated reciprocity, there is no choice on the actor's part whether to cooperate or not. Undoubtedly, exposure is going to impact on sharing to some extent independent, of any partner preferences. Unfortunately, controlling for this effect is far from simple as most control variables could also be preferred traits. Just as it seems unlikely that to assume symmetry based reciprocity has no effect, it also seems unlikely that it could fully account for the patterns of sharing found amongst the Mbendjele.

If we assume that the correlation between association and sharing is the result of partner choice, then we need to consider what advantages this confers. In the previous chapter I discussed explanations beyond exclusive fitness for why kin may be preferred sharing partners. Greater exposure may ensure greater reliability of reciprocation, protecting against defection by allowing donors to keep an eye on co-operators as well as gauging their levels of production. This same argument could be made for non-kin associates.

Alternatively, the correlation between association and cooperation may be the result of reciprocity across multiple domains, not just food sharing.

Amongst the Mbendjele the most prevalent forms of cooperation, besides food sharing, are childcare and cooperative foraging. Cooperative foraging is likely a mutualistic behaviour, as discussed in chapter 3. Furthermore, food sharing is considerably less effective where sharing partners have non-independent variance in productivity. If sharing partners also foraged together this would tend to be the case.

Allocare appears a more likely candidate for a service which could be exchanged out of kind for food. I attempted to test whether allocare also mapped to a similar network as interaction and food sharing. Whilst it is known that unrelated individuals do participate in childcare amongst BaYaka populations, such occurrences were relatively rare in the scan data. Consequently, any correlation between child care networks and either the sharing or association networks is entirely confounded by relatedness. It is unclear whether kin caring for their relative's children are doing so for inclusive fitness benefits, which is of course a strong possibility, or whether even partially it represents a form of reciprocal altruism.

A study on the Tsimane which looked for interaction between different forms of exchange found that food was exchanged for labour, but not childcare or sick care (Jaeggi et al. 2016). The same study found a significant degree of reciprocity between transfers of meat and produce. Whilst meat sharing was largely absent in this population, a number of results are in line with this form of out of kind reciprocity. After controlling for relatedness only male-female associations are a significant predictor of sharing in both camps. Similarly, male network position has a greater impact on sharing than does female position. Potentially, women are directing food towards men outside of their household and unrelated to them, either directly or affinally, as a way to access meat. Clearly, if this is the

case in the short period of data collection this did not pay, though perhaps under different conditions meat sharing is more common.

Setting aside the meals for meat explanation, there is an alternative hypothesis. At an ultimate level this partially unreciprocated sharing may not appear logical, but it could have the underlying proximate explanation. If food sharing is based on a system of attitudinal reciprocity, rather than calculated reciprocity, then transfer of food may occur between pairs with strong social ties, independent of reciprocation. Whilst we might expect attitudinal reciprocity to be less sensitive to unequal exchanger than calculated reciprocity, to maintain the system there must be some degree of contingency. In this case, we would expect unreciprocated sharing to decrease the strength of social ties, in turn reducing sharing. However, this assumes that sharing is the only factor in the formation and maintenance of social ties. This is almost certainly not the case, though the basis of social ties, particularly between unrelated and unmarried men and women, is largely unexplored.

7. Mbendjele children's contribution: Implications for the embodied capital model

7.1 Introduction

Compared to other primates, humans exhibit an extended juvenile period. We wean at an earlier age than other great apes and reach sexual maturity significantly later (Harvey & Clutton-Brock 1988). Amongst primates, age at first reproduction and quality/complexity of diet (operationalised as percentage frugivory) are both positively correlated with brain size (Barton 1999, Walker et al. 2006). Even before such quantitative data was available, the opinion that a long childhood was necessary to acquire the skills and knowledge human foragers rely upon was common (See Blurton Jones & Marlowe 2002 for a number of examples of this common assumption). The "practice theory" (Blurton Jones & Marlowe 2002) has largely been forgotten in the wake of more sophisticated life history models which tie together growth, reproduction, mortality and ecology. However, the Embodied Capital Model (ECM) (Kaplan et al. 2000) retains the focus on the complex foraging niche.

Embodied capital model

Unlike the practice theory, the ECM not only explains the extended juvenile period but also the long human life span and reproductive support by adult males and post-reproductive individuals (Kaplan et al. 2000). It is proposed that these life history traits coevolved with increased intelligence in response to the transition to the complex foraging niche. Central to this theory is the notion that high quality difficult to acquire foods, particularly those targeted by male foragers, are able to produce large energetic surpluses. However, to successfully and efficiently exploit these foods a large prior investment in embodied capital is required. The formal ECM (Kaplan et al. 2000) makes no assumptions as to the type of

embodied capital, only that it accrues with time spent in the juvenile period (Blurton Jones & Marlowe 2002). Growth, learning and socialisation could all constitute investment in embodied capital. However, given that slow growth is a characteristic of the juvenile period in humans (Leigh 2001), proponents of the ECM have tended to focus on the impact of childhood learning on adult productivity (Kaplan et al. 2000, Walker et al. 2002, Gurven et al. 2006).

By suggesting that the extended juvenile period is an adaptation, the ECM shares something in common with reproductive conflict theories of life history (Cant & Johnstone 2008, Moya & Sear 2014), though they conflict in regards to the importance of subsistence. In contrast, the Grandmother Hypothesis (Hawkes et al. 1998) suggests that delayed maturation is not itself adaptive, but a by-product of selection on other life history traits. As with the ECM, a focus is placed on the move to a diet focussed on hard to acquire foods.

Reproductive conflict models (RCM)

Reproductive conflict models argue that human life history evolved to reduce intergenerational competition by avoiding an overlap in reproduction (Cant & Johnstone 2008, Moya & Sear 2014). According to this theory, the relative benefits of individual reproduction versus inclusive fitness vary over the life course, arguably as a result of migration and senescence. Thus, both at an early life stage and late in life it may be optimal to invest in siblings or grandchildren, rather than one's own offspring, leading to the evolution of a late age at first birth (Moya & Sear 2014) and menopause (Cant & Johnstone 2008).

Grandmother Hypothesis (GH)

The GH suggests that, relative to our extended life span, the juvenile period is not actually that long. Thus the relevant evolutionary question is not 'why do humans take so long to reach maturity?' But rather 'why are humans so long lived?' (Hawkes et al. 1998). Hawkes and colleagues argue that a long post reproductive life coevolved with the transition to a complex foraging niche, as women were able to gain inclusive fitness benefits by supporting adult offspring via provisioning and childcare.

These three theories present contrasting views of human childhood. For the ECM it is a period of investment and learning. According to the RCM we would expect children to be concerned with the wellbeing of their siblings and helping their family. Finally, the GH posits childhood as a waiting period and makes no real predictions as to the behaviour of children. In this chapter, we examine the activity patterns of Mbendjele children and compare them to Agta fisher-gatherers. I firstly address the economic contribution of Mbendjele children, before moving on to discuss the extent to which they provide domestic help to their families.

7.2 What is the economic contribution of Mbendjele children and how is this constrained?

The economic contribution of children varies widely depending on culture and environment. In Peru, for example, 49% of children living in a rural setting, who do not attend school, are economically active. In contrast 23% of children living in cities and not attending school engage with economic activities. For children attending school the same pattern is observed, though in both cases the value is considerably lower (urban = 6.8%, rural = 39.7%) (Tienda 1979).

Unsurprisingly, education limits economic participation but clearly it is not the only factor. Limiting our discussion to foragers, there is still considerable cross-cultural variation. Whilst Hadza children forage frequently, !Kung children rarely participate in such activities, perhaps as a result of the greater risks in the !Kung's environment (Blurton Jones et al. 1994).

Whilst there is no consistent pattern in the foraging effort of hunter-gatherer children, levels of productivity reveal a more consistent pattern. Data on several foraging societies, including the Hadza, suggests that throughout childhood and adolescence, hunter-gatherers consume a greater number of calories than they produce (Kaplan et al. 2000). Whether this deficit is a result of physical constraints, a deficiency of skill or a lack of motivation remains an area of debate.

Reef foraging by Meriam children provides evidence of physical constraints on foraging efficiency. Due to their smaller stature, Meriam children are unable to cover the same distance as adults whilst foraging. Consequently, encounter rates with high quality prey are reduced. Children adapt to this by foraging on a broader spectrum of lower quality shellfish (Bird & Bliege Bird 2002).

The impact of learning on foraging efficiency appears to vary considerably both for different populations and different foraging activities. Marine foraging activities by the Meriam showed little evidence of skill related constraints (Bliege Bird & Bird 2002). Similarly, the efficiency of Hadza (Blurton Jones & Marlowe 2002) and Mikea (Tucker & Young 2005) children foraging for plants does not appear to be limited by skill. In contrast hunting skill amongst Ache (Walker et al. 2002) and Tsimane (Gurven et al. 2006) does provide evidence of skill based constraint.

When neither skill nor size appears to constrain foraging efficiency, and yet children's participation remains low, this has been interpreted as evidence of a low incentive of foraging amongst children (Bliege Bird & Bird 2002, Tucker & Young 2005).

Whilst it is likely that both skill and physical capabilities impact on the efficiency of almost all foraging activities, attempts to identify the greater limiting factor are an important step in understanding the evolution of human life history. This is of particular relevance to the embodied capital model. If size, strength or other growth related factors limit the ability to participate in foraging, and this also serves to prevent learning and practice of such activities, then the ECM cannot account for the extended childhood.

To assess the economic contribution of Mbendjele children I reconstructed foraging trips from the scan data, using the same methods as for the adults (outlined in chapter 4). In order to identify whether economic effort by children was under constraint we compared time spent foraging with similar data for the Agta. Across the two populations three broad foraging strategies can be observed. As previously discussed in chapter 1, many of the resources targeted by human foragers require a high level of skill relative to other primates. However, here I classify levels of skill purely within the human foraging niche, thus a low skill foraging strategy is only so in relation to other human foraging strategies. Female foraging is similar in both populations, with a primary focus on the gathering of plant resources such as tubers, fruits and nuts. We categorise this as a low strength, low skill strategy in line with previous studies on similar behaviours (Blurton Jones & Marlowe 2002, Tucker & Young 2005). The second foraging strategy is that of BaYaka men, who preferentially target game and honey. This strategy we define as high strength, high skill (Walker et al 2002, Gurven et al 2006). The final strategy is that of Agta men for whom fishing is the primary economic activity, although hunting and honey collecting are both

also undertaken. We categorise this behaviour as high skill, low strength based on previous work on Peruvian foragers which found boys were able to participate in fishing at an earlier age than hunting (Gurven & Kaplan 2006). Based on this categorisation we make a number of predictions regarding children's foraging effort.

1. If foraging efficiency is constrained by skill, we expect children to engage in high skill activities throughout childhood. Thus, male children should invest more time into economic activities than females.

2. If strength or size constrains foraging efficiency we expect that children should engage in activities with low physical demands.

Furthermore, to examine whether children's foraging effort is motivated more by learning than inclusive fitness we test a third prediction

3. If provisioning rather than learning motivates children to forage we expect little difference between the sexes in foraging effort as both males and females would receive equal inclusive fitness benefits.

7.2.1. Results and discussion

Sample size

Activity data is reported for a total of 469 individuals (Mbendjele male = 41, Mbendjele female = 42 , Agta male = 211 , Agta female = 175). Of these 259 (Mbendjele male = 23, Mbendjele female = 19 , Agta male = 122 , Agta female = 95) are children, i.e. less than 18 years of age.

BaYaka children's foraging effort

Early in life we see a decline in the frequency with which children participate in foraging trips (Figure 1), this is likely a result of increasing maternal independence as they reach an age at which they can be away from their mother for extended periods. The result is interesting firstly as the initial decline suggests mothers are unable or unwilling to completely forego all foraging effort early on in their child's life. Thus, it follows that provisioning by spouses, kin or other camp members are not a sufficient or reliable enough source of calories even for this relatively brief period of time. As the decline occurs relatively quickly this suggests that children are able to separate from their mothers from an early age, though it is unclear whether this is reliant on allocarers.

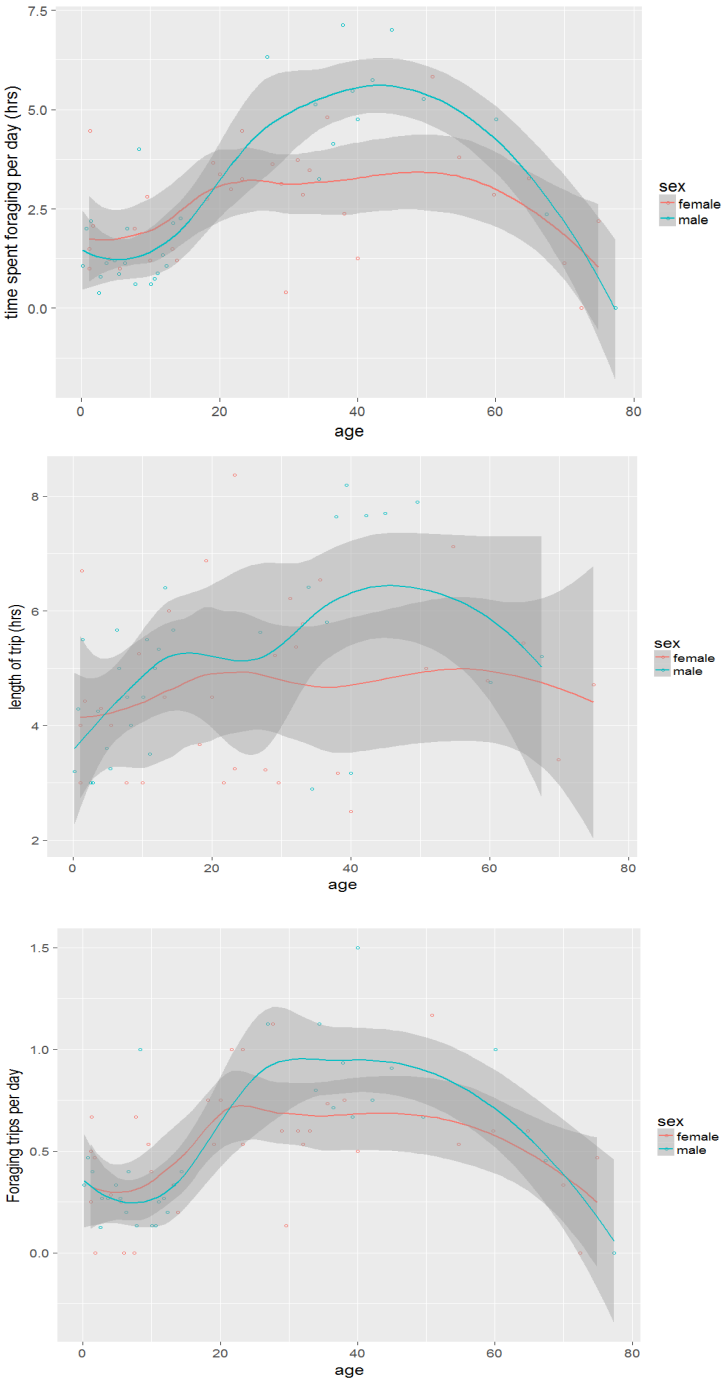

Figure 7.1. Scatterplots of hours spent foraging per day, mean length of foraging trip and number of trips per day against age (years) for Mbendjele females (red line) and males (blue line). Curve fitted using loess. Shaded area represents 95% confidence intervals. N: male = 41, female = 42

Table7. 1. Mean proportion of time spent foraging by BaYaka children of different age ranges. Wilcoxon test of difference between the sexes, significant figures in bold, p values * 0.05, ** 0.005, *** 0.0005

Age group	male mean (sd)	female mean (sd)	W
>3	0.11 (0.07)	0.16 (0.13)	14.5
3-5.9	0.09 (0.01)	0.09 (0.01)	4
6-9.9	0.16 (0.05)	0.20 (0.12)	5.5
10-17.9	0.11 (0.06)	0.09 (0.01)	16

Table 7.2. Mean proportion of time spent foraging by Agta children of different age ranges. Wilcoxon test of difference between the sexes, significant figures in bold, p values * 0.05, ** 0.005, *** 0.0005

Age group	male	female	W
>3	0.12	0.15	396
3-5.9	0.13	0.14	165
6-9.9	0.33	0.19	**154***
10-17.9	0.47	0.33	**363.5***
18+	0.42	0.26	**2160****

During their infancy and early childhood BaYaka children spend relatively little time foraging, at just under 10% of daylight hours (Table 1). Compared to adults, participation in foraging trips is both less frequent and, when it does occur, of a shorter duration (Figure 1). There are no significant differences in proportion of time spent foraging by males and females until adulthood (Table 1).

Agta children's foraging effort

Sexual variation in Agta adult's foraging effort is similar to the BaYaka, with males spending a significantly greater proportion of their time on economic activities (Table 2). In contrast to the BaYaka, this sex difference emerges pre-adolescence (Figure 2).

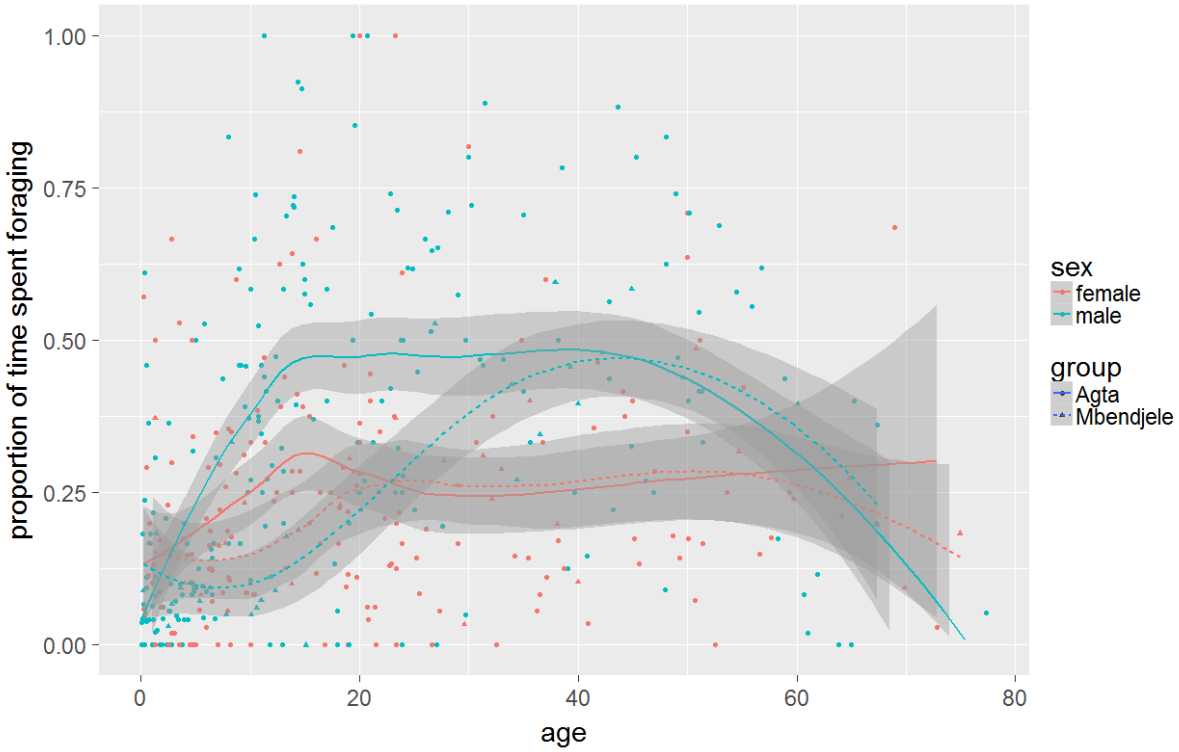

Figure 7.2. Scatterplot showing proportion of time spent on economic activities by Mbendjele (triangles & dotted line) and Agta (circles & solid line) by age (years). Red denotes females, blue denotes males. Curves fitted using loess. Shaded areas represent 95% confidence interval. N: Mbendjele male = 41, Mbendjele female = 42, Agta male = 211 , Agta female = 175

The differences in children's foraging effort between the two populations could be explained as either a difference in motivation or a difference in constraint. The Agta data conforms to our first and third predictions. Boys who partake in the higher skilled activities such as fishing, and thus are more likely to profit from experience, spend a greater amount of time on economic activities than their female peers. This is in line with my first prediction and suggests that learning is a primary motivator of Agta children's foraging

effort. This is not to say that when children forage they are not also make a meaningful contribution to household production. Skill acquisition and provisioning are not mutually exclusive. To properly disentangle the separate effects in cases such as this it would be necessary to analyse the impact of children's engagement in high skill foraging on the fitness of themselves and their families. If learning and provisioning are both motivating factors in the activity of children this provides interesting new theoretical directions in relation to the coevolution of the human foraging niche and life history.

The lack of any difference in foraging between BaYaka males and females until adulthood provides no evidence of a learning motivation. This could suggest that skill has little constraint on Mbendjele foraging efficiency and, thus, our categorisation of BaYaka men's foraging practices as high skill was false. Alternatively, if learning is of importance to hunting, as seems to be the case in other forager populations (Walker et al 2002, Gurven et al 2006), an age-related factor, perhaps size or strength, precludes them from participation.

Unfortunately, our data do not allow a within population comparison of involvement in high skill foraging practices. Whilst the Agta both hunt and fish, they do the former relatively rarely. We can only say that in the population where fishing provides an alternative to hunting, boys spend a greater amount of time foraging than in a population where such an alternative is not present. This mirrors results from a study that was able to compare practices within populations (Gurven & Kaplan 2006). In the Machiguenga and Piro, boys become involved in fishing at an earlier age than they do hunting. Whilst the relatively late age at which boys start hunting in a range of societies is indicative of age related physical constraints (Gurven & Kaplan 2006, Macdonald 2007) we know relatively little of the demands of hunting and why it may be under such constraint. A comparison of the Agta's fishing, with hunting by the BaYaka may provide some insight. Age related

physical factors such as size and strength may constrain hunting activities in two ways: A) They may limit the efficiency of foraging activities so severly that they become unproductive. B) they may entail a high risk to health. Fishing and hunting are both physically demanding and age is likely to impact on efficiency independent of any learning effect for both activities. Thus, if hunting is under greater constraint than fishing, it is likely that this is the result of greater inherent risks.

Greater risk in the environment of !Kung has been used to explain why children in this society spend a smaller amount of time foraging than Hadza children despite the many similarities between these groups (Blurton Jones et al. 1994). The !Kung have to travel larger distances to access food than do the Hadza. Similarly fishing, particularly riverine fishing, tends to occur in closer proximity to camps than does hunting. Additionally, hunting inevitably involves interaction with relatively large and sometimes dangerous animals. It could be that until a certain size or strength threshold is reached the risks of significant injury during hunting are so high as to preclude any participation. As with much work on hunter-gatherer subsistence, this thesis focuses on data collected within camps. To better understand the costs and constraints of foraging, it is necessary to collect data on actual foraging trips. Properly describing how size and strength relate to risk and efficiency are important future steps in understanding how children's behaviour is shaped by the foraging niche.

Our results are not the first to suggest that male specific foraging is under some physical constraint. However, where it differs from previous reports is in the severity of the constraint. The delay in the age at which boys started fishing and when they started hunting in the Peruvian groups was relatively small. In that case, boys began hunting prior to adolescence (Gurven & Kaplan 2006). In contrast, for the BaYaka, increases in foraging

effort only occur during adolescence, presumably coinciding with the increased growth rate at that age. The BaYaka are only a single hunter-gatherer population and it is therefore problematic to interpret this result in a wider context. However, cross-cultural data does suggest that many forms of hunting are only undertaken by teenage and adult males (MacDonald 2007). If hunting generally is under significant physical constraint then this has profound implications for the ECM.

Discussion of the ECM often focuses on hunting, particularly considering males late age of peak productivity (Kaplan et al. 2000). The fact that peak productivity occurs several years after growth has stopped is seen as evidence of continued learning. However, if physical constraints not only prevent hunting, but also learning how to hunt, a late peak in productivity may be the consequence of an extended childhood rather than the cause. This raises the question of whether an inability to participate in hunting also prevents learning how to hunt?

7.3 Are Mbendjele children helpers-in-the-nest?

Running parallel to the discussion on children's economic contribution has been a debate on children's role as helpers at home. In particular, there has been a large focus on children as allocarers (Weisner & Gallimore 1977, Ivey 2000, Crittenden & Marlowe 2008), though participation in other domestic activities, such as cooking and cleaning likely confer similar benefits, both aiding the family directly and freeing up adults to perform different tasks. Typically examples of allocare are interpreted as kin selected behaviour as much of the allocare is between kin, often siblings. However, examples of unrelated children caring for one another do also occur and clearly do not fit the pattern of kin selection. Additionally, a sex bias has been reported in some populations, with female children far more frequently offering care (Crittenden & Marlowe 2008), though other populations exhibit a more equal

distribution (Ivey 2000). The earliest work on “helpers in the nest” in human societies has focussed on females, finding that a first-born female conferred greater benefits to future reproductive success than a first born male (Turke 1988). Similar studies have not found the same effect in other societies (Crognier et al. 2001, Hames & Draper 2004), but nevertheless, combined with the apparent sex bias in caregiving effort, they suggest that learning to mother may be as large a motivation as inclusive fitness.

In comparison to the large body of literature on learning how to forage, little attention has been paid to its importance for other activities. A recent study on the Tsimane found that a range of activities, including childcare and domestic chores, show similar patterns of acquisition as foraging skills (Schniter et al. 2015).

As with foraging effort we predict that where learning is an important motivator of children’s activities, sex differences will be apparent. Where children are motivated by immediate fitness benefits and kin selection we expect boys and girls to engage equally.

7.3.1. Results and discussion

In contrast to foraging effort, sex differences in time investment in domestic activities appear prior to reproductive age (Figure 3). Before ten years of age, mean proportion of time spent on domestic activities is equally low for both sexes, between 0 and 3 % (Table 3). Throughout adolescence there is an increase in domestic activity for both sexes. However, the rate of increase is more rapid for females. Adolescent girls spend a greater amount of time on domestic activities (15%) than do adult men (10%).

Table 7.3. Proportion of in-camp hours spent on domestic activities by age group

Age group	male mean	female mean
>3	0.00	0.002
3-5.9	0.01	0.03
6-9.9	0.03	0.01
10-17.9	0.06	0.15
18+	0.10	0.36

Table 7.4. Proportion of in-camp hours spent at play by age group

Age group	male mean	female mean
>3	0.18	0.22
3-5.9	0.40	0.27
6-9.9	0.32	0.23
10-17.9	0.37	0.15
18+	0.02	0.01

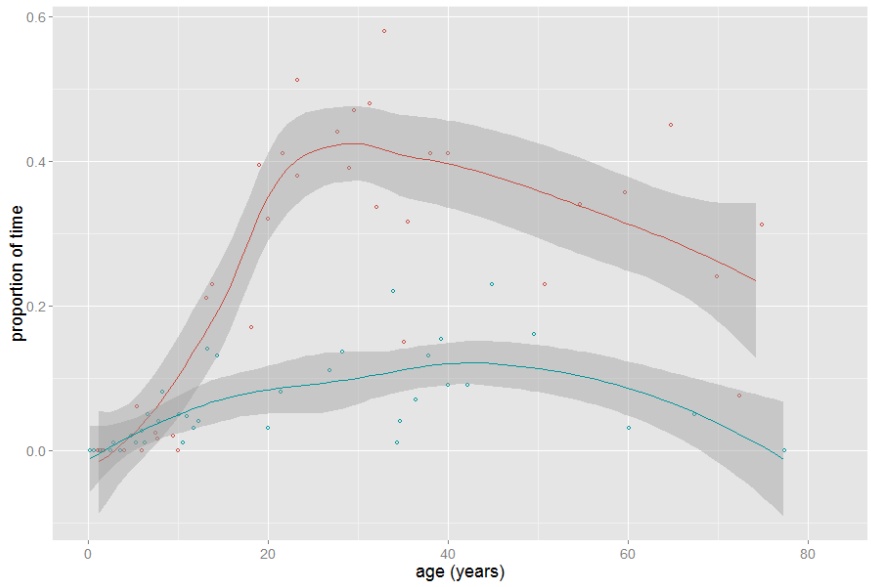

Figure 7.3. Scatterplot of proportion of in-camp time spent on domestic activities by age (years). Red denotes females, blue denotes males. Curves fitted using loess. Shaded areas represent 95% confidence interval.

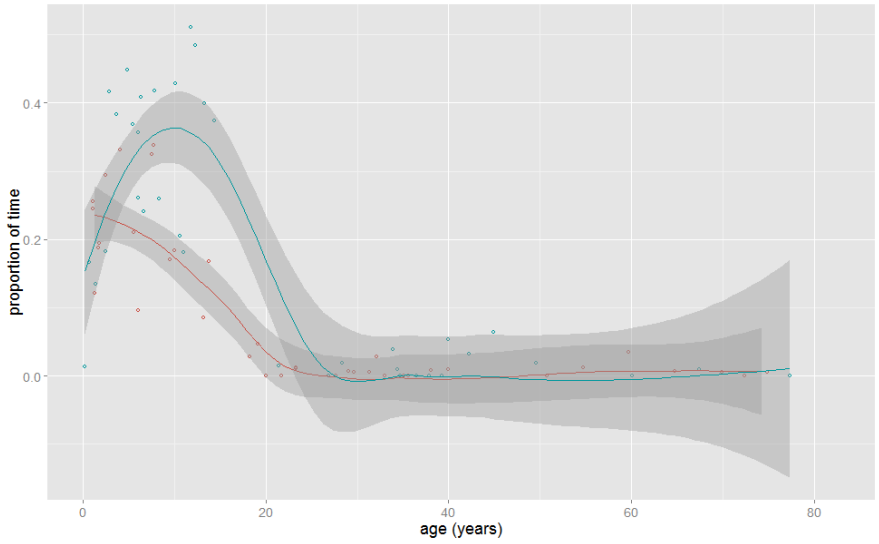

Figure 7.4. Scatterplot of proportion of in-camp time spent at play by age (years). Red denotes females, blue denotes males. Curves fitted using loess. Shaded areas represent 95% confidence interval.

For females, the amount of time spent at play shows a decrease throughout childhood and adolescence (Figure 4). In contrast males increase time spent playing into their teens, taking up around a third of their in-camp hours (Table 4). Whilst the decline in play occurs earlier in females, both sexes display a similarly low level on reaching adulthood.

Children of both sexes, spend a similar amount of time out of camp on foraging trips. Consequently, time spent in camp is similar. On average Mbendjele children spend just over 80% of daylight hours inside the camp. However, how they choose to spend this time differs markedly. Boys spend a large amount of time playing, an activity which likely confers few immediate fitness benefits but may represent a form of investment in embodied capital. In contrast girls engage in child-care, food preparation and manufacture of items such as rugs and baskets. These activities benefit themselves and their families, though the extents of said benefits are unclear from this data. Divergence in behaviour prior to reproductive age is clear evidence that short term benefits to individuals and their kin are not the only motivator of BaYaka children's behaviour. What is unclear from this result is whether boys are trading off the short-term benefits of helping around the house in favour of investing in their own future reproductive success. Alternatively, girls are engaging more heavily with domestic activities and childcare than we would expect from the short-term fitness benefits they confer, but in doing so they themselves are investing in future reproductive potential by accruing the skills necessary to raise a family of their own.

Very little is known regarding the effect of experience and learning on domestic activities. Amongst the Tsimane it has been shown that people perceive such effects, in relation to a broad range of tasks (Schniter et al. 2015). Many of the tasks which BaYaka girls and women participate in more frequently than males are relatively complex, requiring specific knowledge of tools and processes. Weaving of baskets and rugs requires the processing of

specific plants, the memorisation of patterns and significant manual dexterity to perform with the speed and efficiency of the Mbendjele women. In these cases the effect of experience is clearly visible in the end result. Less obvious is the role of experience in food processing and cooking. Much of the food collected by the BaYaka requires intensive processing and the vast range of items brought back to camp are processed in a variety of different ways. It is not difficult to believe that food process, like manufacture has a large experiential component to its efficiency. However, there are other tasks for which experience is likely to play a relatively small role but nevertheless are undertaken almost wholly by females. The fact that relatively simple tasks such as collecting firewood and water are undertaken by female children but rarely by male children, challenges our assumption that a sexual division of labour in children is an indicator of a learning motivation. Though perhaps such tasks have a greater learnt component then is apparent at a superficial level.

There has been much work which reveals children can have a positive effect on their mother's fertility and survivorship of her offspring particularly in agricultural populations (Turke 1988, Crognier et al. 2001, Bereczkei & Dunbar 2002). Less is known about hunter-gatherers. A study on the !Kung found that the sex of children had no effect on a woman's fertility or survivorship of subsequent offspring (Hames & Draper 2004). A study of BaYaka from the Central African Republic found no evidence that children's allocare offset the increased energy expenditure of their presence (Meehan et al. 2013). The authors of this study cite ethnographic evidence that BaYaka children are often only short-term allocarers, usually whilst an adult is present.

Whilst it remains to be shown to what extent female children's activities impact on the fitness of their kin, it is a clearer picture for male children. Whilst to some extent play may

represent a form of care when younger siblings are present, by and large this is a behaviour unlikely to be explained by kin selection.

Play is far from uniquely humans, the juveniles of many mammal and some bird species frequently engage in play. This has led to a large body of literature considering the adaptive significance of play, particularly in light of the energetic costs it incurs. Some have suggested that play confers relatively low costs and therefore does not require an adaptive explanation or that play is a maladaptive by-product of selection for adaptive adult behaviours (Barber 1991). However, there is a considerable body of literature that looks at play as an adaptive form of investment in adult capabilities (Caro 1988, Byers & Walker 1995), though short-term fitness benefits have also been considered (Barber 1991, Fagen & Fagen 2004, Pellegrini et al. 2007). Work on play in nonhuman mammals has focussed on the development of motor skills, whilst for humans, where sociality and cumulative culture are of large importance, a broader developmental explanation for play is often discussed (Bock & Johnson 2004, Boyette 2016).

Our results suggest that there is a trade-off between time spent playing and time spent working. This trade-off occurs earlier for girls than boys as they begin to participate in domestic chores. Similar results have recently been reported for Central African BaYaka (Boyette 2016). The greater tendency for play amongst males has given rise to theories linking play to dominance hierarchies and aggression (Pellegrini & Smith 1998). The fact that the pattern is apparent in the relatively egalitarian BaYaka, combined with Boyette's (2016) finding that rough and tumble and competitive games are relatively rare in this group, presents a challenge to this hypothesis.

Combining the foraging and play results clearly suggests that play may serve as a replacement for direct experience of foraging. We often observed boys making catapults

and hunting small birds in and around the camp. Another frequent game involved one of the boys taking on the role of an animal whilst the others mimed hunting him. Boyette (2016) found that work pretence was amongst the most common forms of play amongst the BaYaka. Indirect support for this theory comes from the association patterns of male play (Figure 7). From infancy to around the age of 10 Mbendjele boys have a wide range of playmates. From 10 years and upwards they exhibit a greater degree of assortativity, playing most frequently with boys of a similar age.

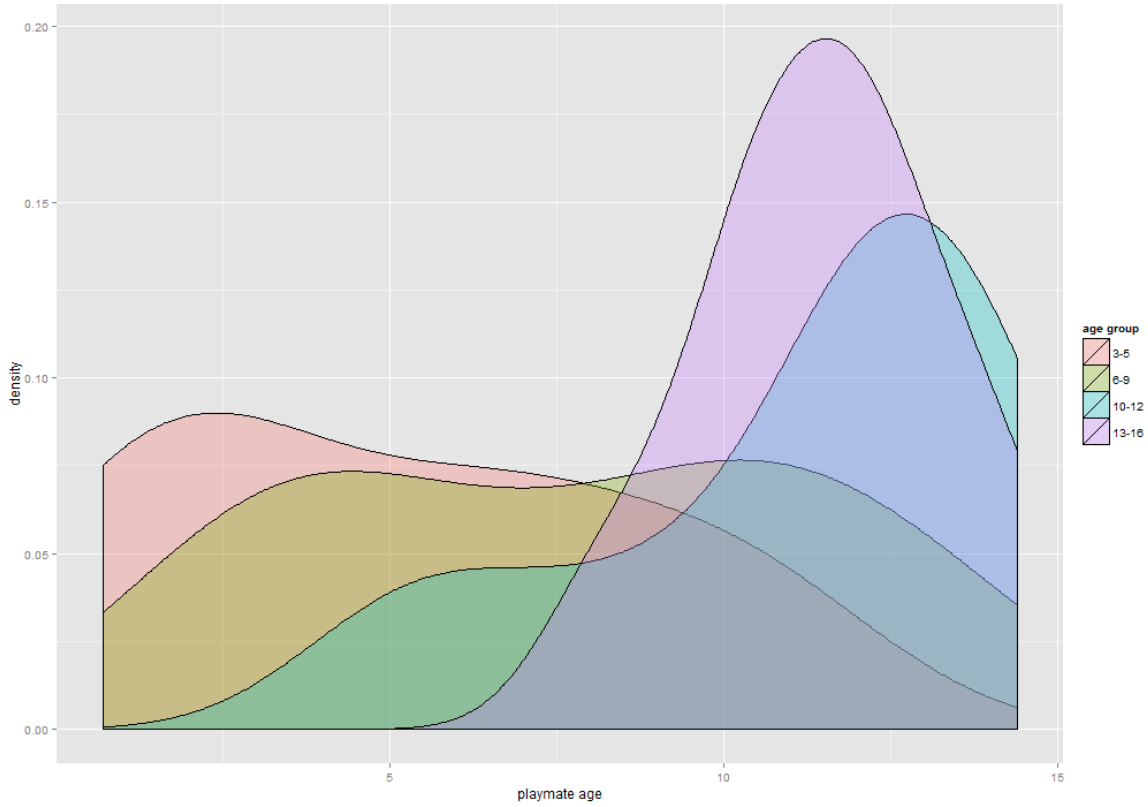

Figure 7.5 Density plot of age (years) of male Mbendjele's most frequent playmates grouped by ego's age group (years). Siblings were excluded.

This assortativity could serve two functions. Firstly, if male-male social ties are particularly important, playing and spending time with similarly aged males during adolescence may constitute investment in social capital. Alternatively, if play amongst male adolescents is a

proxy for direct experience of foraging then it makes sense that those individuals with the same aims would aggregate.

7.4. Conclusion

In this chapter, I present a number of interesting results, the two most important of which are as follows. Firstly, sex differences in behaviour emerge several years prior to reproductive age. Secondly, certain male specific foraging practices are under considerable age related physical constraints. In relation to evolutionary explanations for the extended period of dependence these results are somewhat contradictory. The early emergence of a sexual division of labour, the importance of play and the relatively small contribution of children to household production and domestic chores suggest that learning is a greater motivator of children's behaviour than is inclusive fitness. This is in line with predictions of the ECM over RCM. However, our finding that male specific foraging practices, such as hunting and honey collection, are under significant physical constraint is a considerable challenge to the ECM, at least in its typical formulation.

Male foraging is often positioned as the epitome of the complex foraging niche, and the development of the skills and knowledge to acquire resources such as meat and honey are the selective pressure which extended childhood in humans (Kaplan et al 2000). However, our results suggest that the extended childhood precludes participation in foraging practices such as hunting and therefore may delay skill acquisition. The fact that boys heavily engage in play whilst constrained from taking part in foraging directly suggests that learning is still of importance to male children. However, if play is a poorer alternative to direct experiential learning, than an ECM which focusses on male production cannot explain the extended period of dependency. What then are the alternatives? Our results offer little information in regards to the grandmother hypothesis, which makes very few

predictions regarding children's behaviour. We find relatively little evidence for children making important contributions to the fitness of their mother or siblings, a common finding in forager societies (Tucker & Young 2005, Meehan et al 2013). To some extent this challenges reproductive conflict explanations for a late age at first reproduction (Moya & Sear 2014).

One way that the ECM can be reconciled with these results is if it is correct in attributing a prolonged childhood to investment in embodied capital, but incorrect in its focus on male production. Our results suggest that female domestic tasks and childcare may, like foraging effort and play, be motivated by learning. Whilst more work is necessary to examine the impact of experience on such activities it is important to consider that the extended childhood not only provides the time to develop foraging skills but a whole range of other capabilities.

In combination, the results on male children's economic effort and play provide an interesting avenue for future research. Whilst males did not begin spending a considerable portion of their time foraging until adulthood, there economic participation increases throughout adolescence. During this time, boys will accompany adult females or mixed groups foraging for wild plants. However, they will also begin to accompany adult males, usually their father or grandfather on hunting and honey collecting trips. During our time in Masia one boy of approximately 12 years successfully caught and killed his first duiker whilst out checking snares with his father. Observations such as this suggest that physical constraints do not entirely preclude boys and adolescents from participating in hunting. The limited frequency of their participation may be the result of costs they confer to the adults they accompany. It is not unreasonable to suggest that the younger males cause a decline in foraging efficiency for the whole group by reducing encounter rates as a result of

covering less distance or being less skilled at stalking. Whilst inclusive fitness benefits of aiding younger male kin make up for a decrease in productivity on occasional trips, it perhaps precludes boys from accompanying their family on a regular basis. This sporadic learning amongst adolescent males means that play could serve as a way of pooling and exchanging information. Whilst horizontal transmission of information may be less effective than vertical or oblique transmission, the costs of these latter forms of learning may favour the former. The importance of horizontal learning becomes of even greater importance when we consider that mobility, serial monogamy and high rates of mortality mean that a high proportion of male children will not always be living with their father (Hewlett et al. 2011). A reliance on a few sources of learning would prove highly risky, thus a slower but more reliable system of horizontal learning may evolve.

Quantitative data on who children accompany on foraging trips could provide further insight. If, as we have suggested female activities are not under significant physical constraint, then we would predict girls accompany and work with a wider range of people, of varying degrees of relatedness. Also, data on male productivity could show the relative importance of vertical learning. If horizontal transmission and play are as important as we suggest, then men who grew up with few or no adult male kin present should not exhibit much lower productivity. At this point this theory remains an untested extension of the embodied capital model, suggesting that not only was the transition to the complex foraging niche core to the evolution of an extended period of juvenile dependency, but specifically that physical constraints and a sexual division of labour favoured slower but more reliable means of skill acquisition.

8. Discussion

This thesis set out to address the question of how sociality is used by a group of modern hunter-gatherers to exploit high quality foods. In this final chapter, I address this question whilst providing a summary of the main findings reported in the thesis. I have focussed on three aspects of the subsistence of the Mbendjele BaYaka; the impact of market integration, the function and proximate explanations of food sharing and the interaction between childhood and subsistence, particularly focusing on the motivations and limitations of children's participation in economic activities. The main findings in each of these areas are as follows.

Impact of market integration

The impact of market integration on the subsistence system of the Mbendjele is most obvious in their diet. Despite the fact that foraging remains the primary economic activity, cultivated carbohydrates form a core dietary component - accessed via low effort horticulture, trade or a combination of both. Whilst this shift in diet may have consequences not explored in this thesis, for example relating to health, a focus on these more reliable foods does not appear to have greatly altered the levels of cooperation. Where cooperation has declined, i.e. frequency of meat sharing, this appears to be a result of two factors. Firstly, large scale cooperative hunting has been replaced by hunting with snares and shotguns in small groups or alone. A by-product of this is the disappearance of the formal sharing rules which were required to stabilise this mutualistic cooperation. Secondly, the ability to sell meat to non-Pygmy traders has altered the value curve, so that increasing amounts of meat no longer have diminishing returns for the resource holder.

This leads to lower variance in the fitness value of food and thus the absence of transfers even where large material inequalities arise.

A secondary effect of the change in foraging practices is that the Mbendjele are not only reliant on traders as a source of food and money but also to provide access to the tools they require for hunting. Consequently, in the absence of trade, hunting productivity and the amount of meat in the diet are significantly lower.

Food sharing

Unlike meat sharing, meal sharing remains prevalent and shows a number of similarities in its form across a range of ecological conditions. Meal sharing is common but households retain the majority of food which they acquire (approximately 60%). Sharing is not generalised but targeted at specific sharing partners who are often kin and/or neighbours. Sharing within these dyads reveals high degrees of reciprocity, though this does vary depending on the ecology and structure of the camp.

Meal sharing appears to serve two distinct ultimate functions. Firstly, reciprocal sharing increases individual fitness by buffering against unpredictable shortfalls in production. Secondly, provisioning of kin improves inclusive fitness at a direct cost to an individual. Reciprocal sharing is present under a wide range of ecological conditions and provides the best explanation for previously published data on Mbendjele sharing. In contrast, the presence of kin provisioning is in part a consequence of group structure and perhaps also dependent on access to reliable sources of food.

Not all sharing between kin fits the pattern of provisioning. Relatives also engage in reciprocal sharing. A clear preference for kin as sharing partners, as has been reported for other forager groups (Nolin 2010), was not consistently found for the Mbendjele. Instead,

preference for neighbours and associates (those who frequently interact with one another) was found to have a larger effect.

Whilst at the dyadic level social ties predict the transfer of food, an individual's position within the wider social network has limited impact upon sharing. The exception to this is that men who hold bridging positions within the network (i.e. they score highly for measures of betweeness) receive more food. This may in part result from the fact that men's social ties predict the receipt of food but not the donation. Whilst for women, social ties predict the transfer of food in both directions. This likely reflects the fact that it is women who perform the vast majority of food sharing and therefore is simply the result of attitudinal proximate mechanisms. Alternatively, it could also be the consequence of out of kind reciprocity, particularly given research showing that those men with greater social capital have greater numbers of sharing partners (Chaudhary et al. 2016).

Childhood

Further evidence for the impact of the sexual division of labour was found in the activity patterns of children. In both the Mbendjele and the fisher-gatherer Agta, sexual variation in activity pattern emerges during childhood. For the Mbendjele this is seen in the engagement by girls in domestic tasks around the camp. For the Agta it is participation in foraging which shows substantial variation between the sexes, with males spending significantly more time foraging than similarly aged females. The emergence of sexual variation several years prior to reproductive maturity suggests that learning, rather than immediate or inclusive fitness benefits, motivates the activity of hunter-gather children.

For the Agta participation in foraging begins preadolescence and peak foraging effort for both sexes is reached at around reproductive age. In contrast, significant participation in

foraging begins later for Mbendjele of both sexes, only really increasing upon reaching adolescence. Whilst female Mbendjele reach peak foraging effort at a similar age as the Agta, for men peak effort is found to occur between 30 and 40 years, long after the cessation of growth. Differences in the levels of participation in foraging by Agta and Mbendjele boys may reflect greater age related constraints on the male specific foraging of the Mbendjele, a result of the physical demands and/or risks of activities such as hunting and honey collecting.

Constrained from foraging, Mbendjele boys spend much of their time socialising and at play, whilst girls engage in activities such as child care, cooking and manufacture. This raises questions over the potential function of play and the largely overlooked importance of learning on domestic activities.

These results build on prior work on hunter-gatherer subsistence, particularly research on food sharing (Gurven 2004, Ziker & Schnegg 2005, Nolin 2010, Jaeggi & Gurven 2013, Koster & Leckie 2014, Koster et al. 2015, Dyble et al. 2016) and hunter-gatherer childhoods (Hawkes et al. 1998, Kaplan et al. 2000, Blurton-Jones & Marlowe 2002, Gurven et al. 2006, Boyette 2016). Much of the significance of this thesis relates to the two questions that this work addresses. Namely, why share food? And what is the relationship between diet and the extended period of juvenile dependency? In the following section I will discuss the implication of this thesis and what it suggests regarding future research in these areas.

8.1 Why share food?

The question of why people share food has been a perennial topic in hunter-gatherer studies and increasingly a consensus is being met that reciprocal altruism is a way of buffering risk (Gurven 2004, Ziker & Schnegg 2005, Nolin 2010, Koster et al. 2015).

Contrarily, it is only since the wide acceptance of food sharing as a form of reciprocal altruism that kin provisioning as a simultaneous but independent effect has been given proper consideration (Hooper et al. 2015, Dyble et al. 2016). Food sharing by the Mbendjele clearly fits this multifunctional hypothesis, showing evidence of both reciprocal altruism and kin selection.

Additionally, the results reported in this thesis extend this research on two fronts. Firstly, by highlighting how different forms of sharing have been variously affected by market integration, it is clear that sharing is both multi-formed and multi-functioned and this needs to be fully accounted for. For example, the debate on food sharing is largely based around the assumption that the donor pays an upfront cost for a future benefit, be that reciprocation or inclusive fitness. The primary distribution by the Mbendjele does not conform to this assumption, but actually appears to be the end point of a mutualistic interaction in which all partners receive an immediate benefit.

Previous analyses of Mbendjele sharing have aggregated all types of sharing into a single measure (Jaeggi & Gurven 2014), or else separated meat sharing from other types (Gurven 2004). This would mean that functionally different primary and secondary distributions would be included in the same analysis. The same criticism can be levelled at the analyses in this thesis. Meal sharing was recorded and analysed as a single phenomenon, but our results suggest provisioning and sharing may be two separate phenomena. Given this result and the aforementioned papers (Hooper et al. 2015, Dyble et al. 2016) I suggest that a complementary, qualitative approach to data collection on sharing, with a particular emphasis on identifying differences in the form kin provisioning and reciprocal sharing could prove profitable, allowing us to further tease apart and separately analyse these two behaviours.

The second significant result in regards to the multifunctional hypothesis, is the degree of variation between different camps. Whilst the finding that kin provisioning is reliant upon you living with kin could be regarded as trivial and uninformative, this would be making the mistake of disregarding the importance of how people decide with whom to live. Clearly choosing to live with kin is the first step in investing in inclusive fitness and an absence of kin could be considered as evidence for a lack of kin selection. Given the lack of kin selection on the sharing of the non-integrated Mbendjele, it is necessary to consider that kin provisioning may be a product of horticulture or other predictable supplies of carbohydrates. Again, a more finely grained qualitative approach to meal sharing, looking at differences in the form of sharing as a factor of the relationship between donor and recipient, could serve as a test of this hypothesis.

Where this thesis diverges from previous evolutionary work on human food sharing is in the emphasis on proximate explanations of why people share food. Do people share food because they are able to keep track of and calculate the probable costs and benefits of sharing or simply as a result of their relationship with the recipient? In other words, is sharing calculated or attitudinal reciprocity?

In contrast to experimental approaches (Brosnan & De Waal 2002, Pele et al. 2009, Schino & Aurelli 2010), discriminating between attitudinal and calculated reciprocity for a naturally occurring behaviour is far from simple but the results reported herein do provide some insight. In chapter 4 I argued that the decline in the secondary distribution of meat is a consequence of changes in the value curve resulting from the ability to sell game. This suggests a calculation by the hunter, or his family, with the greater benefits of trade favoured over those of sharing. In contrast, meal sharing appears to persist despite camp wide access to cultigens. When a Mbendjele women shares a plate of manioc with her

neighbour, only to receive a plate of manioc in return ten or twenty minutes later, there appears to be relatively little calculation occurring. Rather an attitudinal rule which says give food to people I like, and dislike people who don't give me food could produce this kind of pattern and still be capable of maintaining a system of reciprocal sharing.

Further evidence for attitudinal reciprocity can be found in chapter 6. Sharing with associates is not in of itself support for attitudinal over calculated reciprocity. However, results which suggest that women share with male associates despite the men lacking the power or motivation to reciprocate could be indicative of an attitudinal mechanism. The persistence of reciprocal sharing even under stable conditions cannot be well explained. The economies of scale argument suggested for the Ache (Gurven et al. 2001) does not hold for the Mbendjele. In contrast, attitudinal reciprocity could account for the persistence of sharing despite the plentiful access to reliable cultigens in both populations.

This raises the question of how can the proximate mechanism underlying sharing be further tested? Lab experiments serve to test whether individuals are capable of calculated reciprocity, but amongst humans this is not the point of contention. Regardless of whether we are capable of calculating and responding to cost-benefit ratios and expectations of other's future behaviour; the question is whether such processes are actually involved when a simpler mechanism may suffice. As such, I believe further work on naturally occurring cooperation provides the greatest opportunity. Detailed longitudinal studies which look at shifts in sharing over time, rather than treating sharing as a single static network, would likely offer some insight. For instance, identifying how participants react to a shortfall or act of defection from a previous sharing partner. However, collection of such data is likely to impose significant challenges. Social network analyses and technology such

as motes may present a partial solution, allowing as they do the collection of longitudinal networks with relative ease.

8.2. What is the relationship between diet and the extended period of juvenile dependency?

Of the three theories that seek to explain the evolution of human childhood discussed in chapter 7, the results in this thesis most directly relate to the embodied capital model (Kaplan et al. 2000). However, the multifunctionality of sharing discussed above does have relevance to the grandmother hypothesis (Hawkes et al. 1998). The debate regarding whether grandmothers or fathers are responsible for the provisioning of hunter-gatherer children has long been tied into discussion of sharing. As such, evidence of reciprocal sharing between unrelated individuals has often been interpreted as evidence against the grandmother hypothesis (Hill & Hurtado 2009). As such the recent resurgence of support for kin provisioning in combination with reciprocal sharing (Hooper et al. 2015, Dyble et al. 2016), could lend greater credence to the GH. However, the results of chapter 5 showing variability in the degree of kin selected sharing, caution against the assumption that food sharing in ancestral populations was multifunctional.

The analyses in this thesis neither conclusively support nor refute the ECM. I argue that the early emergence of sexual variation in activity is a clear indication that learning is a core motivation of hunter-gatherer children. However, the fact that male specific foraging is constrained by age related factors means it cannot easily account for the extended period of dependence. This is not the first research to suggest that male foraging is under constraint (Gurven & Kaplan 2006, Macdonald 2007). Where this research differs is in integrating research on constraints with work on what children do when faced with this limitation. Boys tendency towards play and socialisation over tasks with immediate

benefits to themselves and their family provide further support for the importance of learning in hunter-gatherer childhood. However, an alternative hypothesis not tested in this thesis is that boys are investing not in learning but in forming social bonds. We know that in this population male's social capital is positively correlated with fitness, though we know relatively little about how social capital is garnered beyond the fact that there is a correlation between fathers and sons (Chaudhary et al. 2016). Given the mobility and fluid social structure of hunter-gatherer societies we might assume long term social bonds developed in childhood are of limited value, but given Mbendjele boys preference for same sex, similar aged playmates this is an area which could provide new and interesting insight.

I have suggested that one of the ways that the embodied capital model can be reconciled with age related constraints on foraging is if hunter-gatherer ecology favours indirect and horizontal forms of learning over direct and purely vertical transmission. The underlying logic off this theory is that the former strategy, though perhaps more efficient, is extremely sensitive to paternal absence. Several testable hypotheses can be produced from this theory. Research that looks at the impact of paternal absence/presence during childhood on either skill acquisition or adult productivity would provide information regarding the resilience of hunter-gatherer learning strategies to changes in their social environment. Setting aside the hypothesis that indirect learning has benefits over direct learning; the fact that age related constraints on foraging, and thus presumably direct learning, exist mean that indirect learning may still play a critical role in the development of hunter-gatherer children. The fact that Mbendjele boys spend so much time at play rather than investing in immediately beneficial activities indicates it may serve a learning function. Play may simply act as a proxy to direct participation in foraging, for instance aiding in the development of motor skills and physical stamina. However, if play acts not only as a form of practice but,

as I argued in chapter 7, as a pooling of horizontally and obliquely acquired knowledge, then we would expect play to facilitate information transfer. Again, a more qualitative approach to play than has been used in this thesis could prove useful in this respect. Adam Boyette's work on play by Aka and farmers in the Central African Republic (Boyette 2016) provides some indication of the types of play Aka children participate in and how this compares with non-Pygmies, but extrapolating levels of information transfer from such data would be a matter of conjecture. An alternative approach would be to estimate information transfer networks using measurable socially learnt information, in the same manner as has been done for plant knowledge in this population (Salali et al. 2016). Thus, gauging whether children who play together are more likely to share knowledge.

8.3. The modern hunter-gatherer

In addition to the implications to our understanding of cooperation and social learning, an emergent theme of this thesis has been the variation and complexity of hunter gatherer subsistence. Food sharing is not a single phenomenon but multiple behaviours, varying in both form and function. Levels of kin selection and reciprocity vary considerably as a result of ecology and social structure. The childhood of the Mbendjele varies greatly from that of the Agta, or any other hunter-gatherer group. The social foraging niche is distinguished as much by its flexibility as its common factors. This not only has implications for the use of hunter-gatherers in evolutionary studies, but also wider social implications.

The rights of hunter-gatherers are often contingent on them adhering to an idealised and static view of the forager lifestyle. The Mbendjele BaYaka clearly do not conform to such a stereotype and probably there is no foraging society which does. For the participants in this study, engagement in trade and use of modern technology is integral to their way of life.

These are modern people and just as researchers have to take this into account so should policy makers.

Whilst the primary aim of this thesis was not to provide advice on conservation and land use policy, I believe that it is fair to suggest positive directions for future work in this area. Of greatest importance, I believe, is that legislation should be designed around contemporary hunter gatherers and their modern way of life. This means not only allowing hunting rights and access to land, but also allowing them to use the hunting techniques which are currently practiced. What is clear from this study is that when prevented from using tools such as firearms and snares the Mbendjele do not revert to a more "traditional" way of life. By criminalising the hunting practices of the Mbendjele a conflict between the Mbendjele, local authorities and conservationists is set up whilst simply reinforcing the relationship between the Mbendjele and black-market bush meat traders. An alternative option is to allow Mbendjele to use modern hunting techniques but encourage them to do so in a sustainable manner. An example of this may be to provide them with access to plastic snares, which may cause less harm to particularly sensitive species such as gorillas and chimpanzees than the wire snares they currently use.

8.3 Conclusion

Much of current evolutionary anthropology is concerned with the evolution of cooperation and culture. In analysing the subsistence of a population of hunter-gatherers this thesis illustrates just how important these traits are to human ecology. A reliance on sociality does not differentiate hunter-gatherer subsistence form other human populations, the same can be said for agricultural, pastoralists and industrial societies. Recent changes in the subsistence of the Mbendjele serve to highlight the reliance on sociality. Even as we see a decline in forms of cooperation such as meat sharing and the disappearance of

cultural practices such net hunting, these are replaced with new social strategies, most notably an increasing reliance on outgroup trade, labour and political relationships.

The ultimate benefits of cooperation and social learning are relatively clear but proximate mechanisms remain poorly understood. A greater understanding of the modes of transmission of social learning and the strategies adopted by co-operators has great potential to explain the scarcity of such behaviours in non-human animals. The specialisation allowed by a sexual division of labour, permits long term investment in social learning but such a strategy incurs its own costs. A reliance on learnt skill ensures a prolonged period of low productivity, whilst a sexual division of labour effectively halves the number of sources of learning.

The hypothesis that reciprocal altruism is rare in non-human animals due to cognitive demands is frequently discussed, but less attention has been paid to simpler but no less effective mechanisms of reciprocity, particularly in studies on humans. Food sharing exhibits patterns that suggest elements of both calculated and attitudinal reciprocity, suggesting a need to reappraise both the aforementioned hypothesis and the classification of proximate mechanisms of reciprocity.

This thesis set out to answer the question of how a population of modern hunter-gatherers use social means to exploit high quality foods. The approach taken was to examine behaviours at both the ultimate and proximate level, looking at not only why certain strategies are adopted, but also how. The use of sensing technology and social network analysis has allowed us to see the underlying relationships which facilitate cooperation and social learning. A conclusion which unifies to the two central findings that 1) food sharing acts to reduce variance in productivity, utilising a form of reciprocal altruism suggestive of an attitudinal mechanism, and 2) That social learning of foraging is based upon horizontal

transmission, as well as vertical and oblique pathways, is that social structures as well as social behaviours are critical to the Mbendjele's exploitation of high quality foods. The results in this thesis suggest that affiliative relationships are key to maintaining the reciprocal cooperation and social learning needed to exploit the hunter-gatherer dietary niche and further research in this direction has considerable potential to further elucidate the evolutionary history of the social foraging niche.

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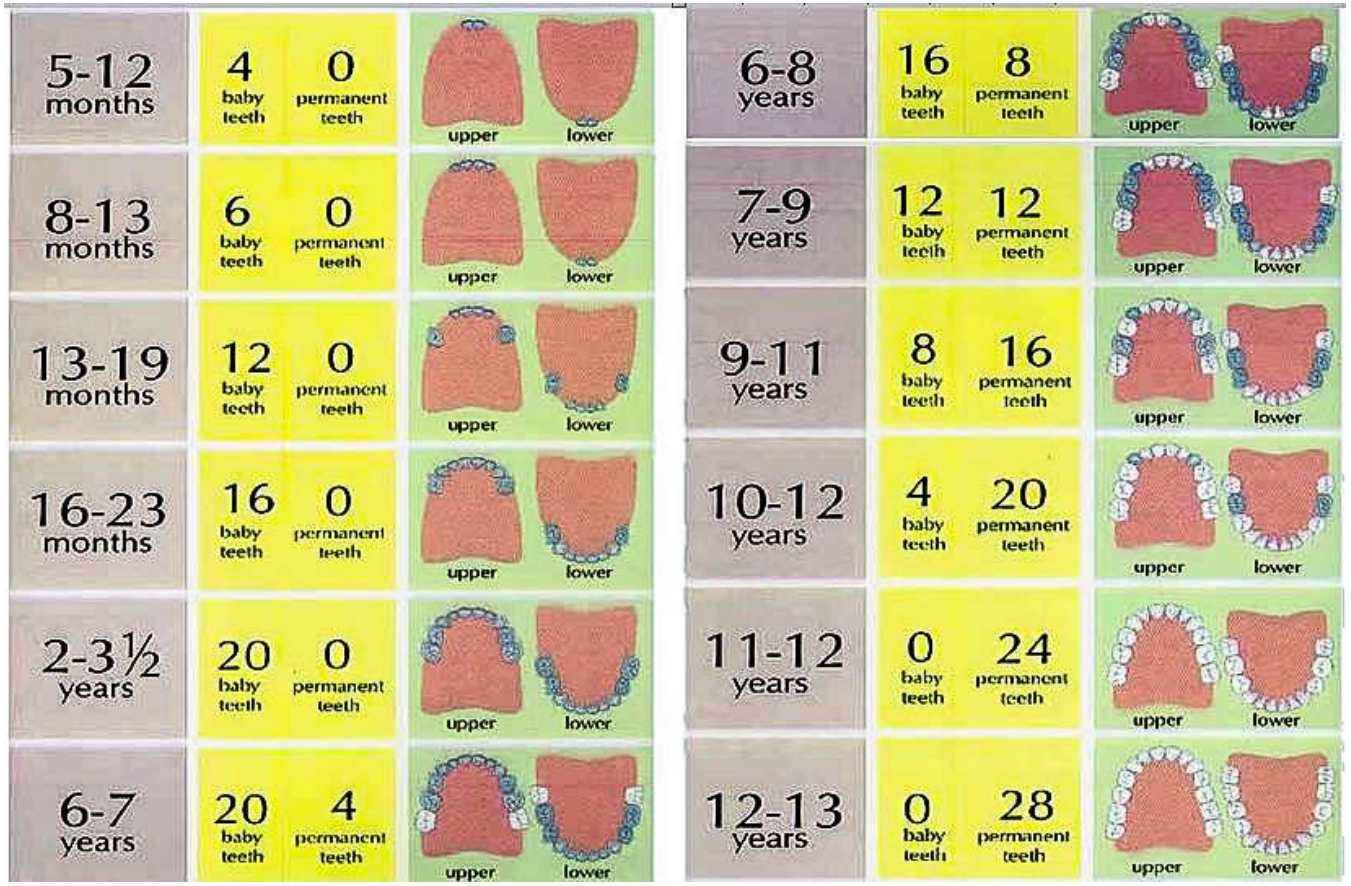
Appendices

Appendix 3.A. Chart used when designating a child's dental age.



Appendix 3.B. Energy values (Kcal/100g) for foods consumed by the Mbendjele

Food	Kcal/100g	source
cassava	160	USDA
meat	116	USDA
banana	89	USDA
plantain	116	USDA
rice	97	USDA
babatini (wild fruit)	97	USDA
kana (wild nut)	407	Boesch & Boesch 1982
palm nut pulp	527	FAO
palm nut kernel	609	FAO
avocado	161	USDA
bread	267	USDA
djabuka	91	FAO
honey	326	FAO
maize	136	FAO